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Shape variation in the talus and medial cuneiform of chimpanzees and bonobos

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Table of contents

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List of figures

List of tables

Abstract

Establishing form-function relationships between anatomy and locomotor behaviours in extant taxa provides critical context for interpretations of extinct species. This study used 3D geometric morphometric methods to explore talus and medial cuneiform shape variation among taxa in *Pan* and to determine whether and to what extent any shape variation may be related to differences in climbing behaviour. Current locomotor behaviour data suggest that bonobos, western, and eastern chimpanzees do not differ from one another in total frequencies of arboreality as much as once thought. However, these data do suggest that bonobos and eastern chimpanzees more often use smaller diameter substrates (<10 cm) when climbing, while western chimpanzees tend to climb larger diameter (>15 cm) tree trunks and boughs. The morphology of the talus and medial cuneiform in *Pan* was predicted to reflect differences in locomotor behaviour, showing a greater emphasis on hallucial grasping in bonobos and eastern chimpanzees, and on an inverted foot set in western chimpanzees. This difference in emphasis was expected to be more pronounced between bonobos and western chimpanzees, both of which appear to climb more frequently than do eastern chimpanzees. The results of this study suggest that the shapes of the bonobo talus and medial cuneiform covary as a functional unit that emphasizes hallucial grasping in the medial cuneiform but not inversion at the talocrural joint. The exact opposite pattern was observed in western chimpanzees, with features that emphasize inversion at the ankle joint but not hallucial grasping. Eastern and central chimpanzee (and possibly Nigeria-Cameroon chimpanzee) talus and medial cuneiform shapes fall in between these two extremes. Overall, these results are reasonably consistent with the different styles of arboreality observed in bonobos and western chimpanzees. Interestingly, the pattern of

covariance observed in this study among chimpanzees and bonobos does not exist in modern humans. If the pattern of covariance observed in *Pan* also characterized the *Pan-Homo* ancestor, then it must have become dissociated at some point during early hominin evolution in order to produce the combination seen in modern humans (i.e., an everted foot set combined with an adducted hallux).

Introduction

The evolution of bipedality is one of the most significant events in human evolutionary history, although, many extinct hominin species are thought to exhibit a combination of adaptations for both terrestrial and arboreal locomotor behaviours (Jungers and Stern, 1983; Stern and Susman, 1983; Ward, 2002; Harcourt-Smith, 2016). Hominins were once a diverse group in terms of anatomy and behaviour (Aiello and Dean, 2002; Harcourt-Smith and Aiello, 2004; DeSilva et al., 2018); however, the only extant hominin species is *Homo sapiens* and this taxon reflects very little of the breadth of variation that once existed in the hominin family. Interpretations of extinct hominin locomotor behaviour typically rely on comparisons of fossil hominin anatomy with that of extant humans and great apes (Stern and Susman, 1983; Kidd et al., 1996; Richmond et al., 2001; Jungers et al., 2009; Lovejoy et al., 2009; Harcourt-Smith et al., 2015). In this regard, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are especially important because they are more closely related to modern humans than any other extant primate (Ruvolo et al., 1991; Goodman, 1999; Salem et al., 2003).

Hominin foot bones are of particular interest to evolutionary studies because they have become increasingly specialized over the course of hominin evolution for balance and support as well as efficient weight transfer during walking and/or running bipedally (Latimer et al., 1987;

Harcourt-Smith and Aiello, 2004; Jungers et al., 2009; Lovejoy et al., 2009; DeSilva et al., 2018). Chimpanzees and bonobos are terrestrial knuckle-walkers and highly proficient climbers (Doran and Hunt, 1994). While the pedal morphology of chimpanzees and bonobos probably reflects adaptations to both terrestrial and arboreal locomotor behaviours, the mechanics of the *Pan* foot and ankle are not fully understood (Holowka et al., 2017a, b). Nevertheless, chimpanzee-like features in hominin foot fossils are often interpreted as retained adaptations to arboreality (Stern and Susman, 1983; Kidd, 1999; Lovejoy et al., 2009; Harcourt-Smith et al., 2015) whereas human-like features are typically interpreted as adaptations to terrestrial bipedality (Latimer et al., 1987; Jungers et al., 2009; Harcourt-Smith et al., 2015). Because interpretations of hominin fossils rely on such comparisons, it is important to establish strong form-function relationships between chimpanzee and bonobo anatomy and their locomotor behaviours.

Chimpanzees and bonobos diverged from one another approximately 1 to 2 million years ago (Prufer et al., 2012; Prado-Martinez et al., 2013; Lobon et al., 2016; de Manuel et al., 2016). Bonobos live exclusively to the south of the Congo River and have been almost completely isolated from chimpanzees (de Manuel et al., 2016), who live on the north side of the Congo River, since their divergence (Takemoto et al., 2015) (Figure 1). There are four currently recognized subspecies of common chimpanzee that are split into two groups. A western group includes the western chimpanzee (*Pan troglodytes verus*), and the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*), while a central/eastern group includes the central chimpanzee (*Pan troglodytes troglodytes*), and the eastern chimpanzee (*Pan troglodytes schweinfurthii*) (Prado-Martinez et al., 2013). These two groups diverged from one another

approximately 600 thousand years ago (Prado-Martinez et al., 2013; Lobon et al., 2016; de Manuel et al., 2016), followed by the divergence of western and Nigeria-Cameroon chimpanzees around 250 thousand years ago (de Manuel et al., 2016). Finally, the two most closely related extant *Pan* subspecies, eastern and central chimpanzees, diverged from one another about 150 thousand years ago (Lobon et al., 2016; de Manuel et al., 2016) (Figure 2).

Western chimpanzees are found to the west of an arid region called the Dahomey Gap, which is uninhabited by chimpanzees, divides the Upper and Lower Guinean Rainforest (Norris et al., 2010), and is thought to act as a barrier between modern populations of western and Nigeria-Cameroon chimpanzees (Pilbrow, 2006; Gonder et al., 2006; Mitchell et al., 2015). Western chimpanzees inhabit the last-remaining fragments of the Upper Guinean Rainforest (Boesch and Boesch, 2000; Norris et al., 2010; Matsuzawa, 2011) as well as savanna and woodland habitats near the edges of their range (Pruetz et al., 2006). To the east of the Dahomey Gap in Nigeria and to the north of the Sanaga River in Cameroon, Nigeria-Cameroon chimpanzees inhabit the Lower Guinean Rainforest within the Congo Basin (Serckx, 2014). They are separated from central chimpanzees by the Sanaga River, which runs in between the eastern extent of the Guinean Rainforests and the western extent of the Congo Rainforest (Mitchell et al., 2015), and possibly other ecological factors as well (Gonder et al., 2006; Mitchell et al., 2015). Central chimpanzees live in the Congo Rainforest south of the Sanaga River and west of the Congo River and Ubangi River (Maisels et al., 2016), which may act as a geographic barrier separating them from eastern chimpanzees (Pilbrow et al., 2006). Finally, eastern chimpanzees primarily inhabit the Congo Rainforest north of the Congo River and east of the Ubangi River, ranging as far east as the Great Rift Valley into drier, woodland habitats

(Gonder et al., 2006). While chimpanzee subspecies are currently separated by modern geographic barriers, the analysis of microsatellite DNA from populations across the entire chimpanzee range has shown that the four subspecies exhibit clinal variation as a result of recent (within the current interglacial period) overlaps in geographic range (Lester et al., 2021).

Despite the Congo River, a major geographic barrier separating bonobos and chimpanzees, genetic analysis has revealed some evidence of ancient interbreeding between bonobos and the geographically proximate central and eastern chimpanzees (de Manuel et al., 2016). Relatively more recent interbreeding events have also been identified between central and Nigeria-Cameroon chimpanzees (Mitchell et al., 2015; de Manuel et al., 2016) as well as between central and eastern chimpanzees (de Manual et al., 2016). For instance, there is some genetic overlap between the Nigeria-Cameroon and eastern/central genetic groups in the transitional zone between the Guinean and Congo Rainforests, where there has likely been a low rate of migration between Nigeria-Cameroon and central chimpanzees across the Sanaga River (Mitchell et al., 2015). Western chimpanzees and bonobos are less genetically diverse than Nigeria-Cameroon, central, and eastern chimpanzees (Fischer et al., 2011; Prado-Martinez et al., 2013, Lester et al., 2021). Evidence of ancient interbreeding, as well as ancient introgression from bonobos have been documented in Nigeria-Cameroon, central, and eastern chimpanzees, but not western chimpanzees (de Manuel et al., 2016). Some researchers have suggested that western chimpanzees should be elevated from subspecies to species level based on genetic and biogeographical data (Morin et al., 1994; Gonder et al., 2011).

Chimpanzee habitats range from lowland evergreen and semi-deciduous rain forests with low seasonality to highly seasonal and dry forest and savanna mosaics (Watts, 2012; Boesch et

al., 2019). In contrast, bonobos live predominantly in lowland evergreen rain forests, with some populations inhabiting drier habitats to the southern and eastern edges of their range (Serckx, 2014). Bonobos and all chimpanzee subspecies are highly frugivorous and climb trees in order to access their preferred food: ripe, fleshy fruits (Nishida and Uehara, 1983; McGrew et al., 1988; Serckx et al., 2015). Even eastern and western chimpanzee communities living in territories dominated by grasslands with only a small fraction of forested area are known to consume a disproportionately large amount of food from the forests within their territory (McGrew et al., 1988; Piel et al., 2017).

Chimpanzees generally experience pronounced fruit shortages each year, and some communities in drier habitats must rely heavily on fallback foods (Nishida and Uehara, 1983; McGrew et al., 1988; Pruetz, 2006; Watts et al., 2012; Piel et al., 2017). Fallback foods are defined as foods whose consumption is inversely related to the consumption of fruit and the kinds and amounts of these foods that are consumed are highly variable among chimpanzee communities (Matthews et al., 2019). Fallback foods are often more difficult to digest and less rich in nutrients compared to the preferred fleshy fruits, from which chimpanzee and bonobo digestive systems more readily extract high quality nutrients (Matthews et al., 2019). In contrast, bonobos generally have greater access to ripe, fleshy fruits year-round due to the lower seasonality of their habitat (White and Wrangham, 1988). Despite the more consistent access to fruit, terrestrial herbaceous vegetation, including leaves, stems and shoots, are not fallback foods for bonobos, but are instead also eaten year-round (Malenky and Wrangham, 1994).

Long-term studies on habituated communities are essential for comparing behaviours between populations as well as between taxa (Boesch et al., 2019). Such studies have been

established in the rainforests of the Tai Forest (Ivory Coast) and at Bossou (Guinea) on fully habituated western chimpanzees (Boesch et al., 1978; Boesch et al., 2019). The Fongoli study site in Senegal was the first site to habituate savanna-living western chimpanzees (Bogart and Pruetz, 2011). There are no long-term study sites within the range of Nigeria-Cameroon chimpanzees nor are there sites where they are fully habituated (Kamgang et al., 2018; Abwe et al., 2019). The oldest long-term chimpanzee study sites are in Tanzania at Gombe (Goodall, 1968; Goodall, 1986; Pusey et al., 2007; Wilson et al., 2020) and Mahale (Nishida and Uehara, 1983; Nakamura and Nishida, 2012). Both of these study sites are situated in the far eastern range of the eastern chimpanzee and are in woodlands rather than rainforest. Other long-term eastern chimpanzee study sites are in Uganda within the Congo Rainforest at Kibale (Watts, 2012) and Budongo (Reynolds, 2005). Well-habituated central chimpanzee communities are located in the tropical rainforests at Goualougo and Ndoki in the Republic of Congo (Morgan et al., 2006; Musgrave et al., 2020), and in the coastal forest at Loango in Gabon (Boesch et al., 2009; Pika et al., 2019). There are two major bonobo study sites with fully-habituated communities in Wamba (Kano, 1980; Terada et al., 2015) and LuiKotale (Hohmann and Fruth, 2003; Hohmann et al., 2019). Another major site, Lomako, is home to communities of semi-habituated bonobos (Badrian and Badrian, 1981; Brand et al., 2016). All three of these study sites are situated in the Congo Rainforest within the Democratic Republic of Congo; however, there are populations living in drier forest at the edges of the bonobo range (Serckx, 2014; Pennec, 2016).

Locomotor behaviour in bonobos and chimpanzees

The locomotor behaviours of three populations of chimpanzees and two populations of bonobos have been quantitatively studied (Susman et al., 1980; Susman, 1984; Hunt, 1989, 1992, 1994; Doran, 1992, 1993a, b; Ramos, 2014). These studies were conducted in the Tai Forest (Doran, 1992, 1993a, b), Gombe and Mahale (Hunt, 1989, 1992, 1994), LuiKotale (Ramos, 2014), and Lomako (Susman et al., 1980; Susman, 1984; Doran, 1993a). Lomako is the only one of these sites where the community was not fully habituated to humans when the research was conducted (Doran, 1993a). Early reports of bonobos in the wild gave general and conflicting descriptions of their locomotor behaviour. For example, Nishida (1972) reported that bonobos spent their days on the ground to get out of the heat whereas Badrian and Badrian (1977) reported that bonobos were more arboreal than chimpanzees.

The first quantitative study of bonobo locomotion was conducted at Lomako over a four-week period in February-March of 1979 (Susman et al., 1980). At the time, poor habituation of the bonobo community limited the researchers in their descriptions of arboreal locomotion, as the apes would flee into the trees or remain on the ground but quickly disappear from sight upon spotting human observers (Susman et al., 1980). Additional data collected between November 1980 and June 1982 was also published (Susman, 1984). A ten-month study from December 1986 to October 1987 at Lomako later reported that bonobos not only feed arboreally but also travel between feeding sites arboreally (Doran, 1993a). Again, a lack of habituation in the observed bonobos prevented researchers from determining the proportion of time they spent in the trees (Doran, 1993a). Nevertheless, bouts of arboreal travel between sites up to 1.7 km apart were considered enough evidence to tentatively conclude that bonobos were in fact more

arboreal than chimpanzees (Doran and Hunt, 1994), as this kind of arboreal travel had never been observed in chimpanzees (Doran, 1993a). Although subsequent research used data collected from the 1986-87 study at Lomako to compare the locomotor behaviours of chimpanzees and other great apes to bonobos (Doran and Hunt, 1994; Doran, 1996, 1997), no further results from fieldwork focused on terrestrial and arboreal locomotor behaviour in wild bonobos was available until 2014 (Ramos, 2014). Based on a study conducted in two six-month periods (from June to December of 2010 and from January to May of 2012) of a fully habituated community at LuiKotale, it was concluded that bonobos are equally or perhaps even less arboreal than are eastern and western chimpanzees (Ramos, 2014).

Arboreal quadrupedalism, as well as climbing and scrambling were the most frequently observed arboreal locomotor behaviours in all four studies (Susman et al., 1980; Susman, 1984; Doran, 1993a; Ramos, 2014). The earlier studies (Susman et al., 1980; Susman, 1984) observed that quadrupedalism was the most common behaviour; however, Doran (1993a) and Ramos (2014) both observed climbing and scrambling more frequently than arboreal quadrupedalism. The frequencies of suspensory behaviour as well as leaping and diving decreased in each subsequent study, which is likely an effect of greater habituation (Susman et al., 1980; Susman, 1984; Doran, 1993a, 1996; Doran and Hunt, 1994; Ramos, 2014) (Table 1). The LuiKotale fieldwork benefitted from observations of a fully habituated bonobo population and was thus able to compare the overall amount of time bonobos spent on the ground during the day as opposed to in the trees (Ramos, 2014) (Table 2). Compared to the earlier studies at Lomako, considerably more climbing and scrambling and less arboreal quadrupedalism was observed in bonobos at LuiKotale and no significant arboreal travel between feeding sites was observed

(Ramos, 2014). Somewhat unexpectedly, the fully habituated bonobos of LuiKotale travelled terrestrially 98% of the time (Ramos, 2014). Ramos (2014) reasoned that the earlier observations of greater arboreality at Lomako were most likely a response to the presence of a perceived threat from the human researchers, as the fully habituated bonobos of LuiKotale never travelled between feeding sites arboreally. These new data from LuiKotale also showed that male and female bonobos spend roughly half of their waking time in the trees and the other half on the ground (Ramos, 2014). In terms of the overall time spent in the trees, bonobo males and females are no more arboreal than are male and female chimpanzees in the populations studied to date (Doran and Hunt, 1994; Ramos, 2014).

Quantitative studies focusing on the locomotor or postural behaviour of wild chimpanzees have been limited to western and eastern chimpanzees. The first quantitative field study was conducted in 1986-87, with observations of two fully habituated eastern chimpanzee communities from Mahale and Gombe spanning the wet and dry seasons (Hunt, 1989). Positional data were analysed with the goal of resolving debates over chimpanzee skeletal morphology, specifically whether their skeletons were specially adapted to brachiation (like gibbons) or to other behaviours such as vertical climbing (Hunt, 1991). Between March and September 1988, the first quantitative field study of western chimpanzee locomotor behaviour on a fully habituated population in the Tai Forest was conducted (Doran, 1992, 1993a, b). In combination, these data provided insight into both arboreal and terrestrial locomotor behaviour for western and eastern chimpanzees (Hunt, 1989; Doran, 1992, 1993a, b). The only significant difference in locomotor behaviour between the eastern chimpanzees at Gombe and Mahale is that Gombe chimpanzees spend slightly more time in the trees than do Mahale chimpanzees (Doran

and Hunt, 1994). Western chimpanzees in the Tai Forest, however, spend more time higher up in the trees and climb more frequently than eastern chimpanzees (Doran and Hunt, 1994).

Currently, the best data for comparing western and eastern chimpanzees as well as bonobos derive from fieldwork at Mahale, the Tai Forest, and LuiKotale, respectively, because communities observed in each study were fully habituated and the results of each study were designed (Ramos, 2014) or were modified (Doran and Hunt, 1994) with the goal of making comparisons between species, subspecies, and populations. The data deriving from the fieldwork at Mahale, the Tai Forest, and LuiKotale indicate that the most common arboreal locomotor behaviour in bonobos, western, and eastern chimpanzees is climbing and scrambling, followed by arboreal quadrupedalism (Table 3). More than 70% of the arboreal locomotor activity of bonobo males and females as well as Tai males is spent climbing or scrambling (Doran and Hunt, 1994; Ramos, 2014). In comparison, climbing and scrambling makes up around 59% of the arboreal locomotor activity of Tai females as well as male and female eastern chimpanzees (Doran and Hunt, 1994; Ramos, 2014). Tai females and eastern chimpanzees most frequently engage in arboreal quadrupedalism whereas Tai males engage in arboreal quadrupedalism least frequently (Doran and Hunt, 1994).

Habituated bonobos at LuiKotale are less suspensory and leap and dive less than Mahale and Tai chimpanzees, but move bipedally more often (Ramos, 2014). This is surprising considering that bonobos have impressive leaping abilities (Scholz, 2006), which were most recently documented in semi-habituated bonobos in the Manzano Forest, Bolobo Territory in the Democratic Republic of Congo (Druelle, 2020). However, like in earlier studies (Susman et al., 1980; Doran, 1993a; Ramos, 2014), Druelle (2020) suggested that behaviours like leaping that

allow bonobos to remain in the trees rather than descend to the ground represent a response to perceived threats, such as the presence of humans. Moreover, the number of ground-level observations of bonobos is correlated with the habituation level of their community (Narat et al., 2015). In combination, these field studies of bonobos suggest that fully habituated bonobo communities will be observed on the ground more often than un- or semi- habituated communities (Ramos, 2014; Narat et al., 2015; Druelle, 2020).

The size of the weight-bearing substrate used during arboreal quadrupedalism has an effect on the locomotor strategy employed in all three taxa studied to date. Doran (1993a) observed that western chimpanzees and bonobos more often engage in palmigrade quadrupedalism on thinner substrates and knuckle walk on sufficiently wide, and horizontal, arboreal substrates. Comparing knuckle-walking and palmigrade quadrupedalism on arboreal substrates, western chimpanzees knuckle walk far more frequently than either eastern chimpanzees or bonobos, both of which appear to favour palmigrade quadrupedalism (Doran and Hunt, 1994). Early studies at Lomako reported that approximately 93% of the arboreal quadrupedalism observed over a period of four weeks was palmigrade and that it usually occurred on substrates up to 25 cm in diameter (Susman et al., 1980). Later studies at Lomako were similar, in that 83% of male and 87% of female bonobo arboreal quadrupedalism was palmigrade (Doran, 1993a). At LuiKotale, however, Ramos (2014) did not differentiate between these two forms of arboreal quadrupedalism.

In 94% of climbing bouts, bonobos at LuiKotale utilized thin (2 to 10 cm in diameter) substrates, such as small trees and vines, as opposed to wider tree trunks (>10 cm) (Ramos, 2014) (Table 4). In fact, LuiKotale bonobos were observed to use small diameter substrates for

climbing, predominantly in a rope-climbing style requiring both the hands and feet to grasp a small substrate, even when larger diameter substrates were visible (Ramos, 2014). However, in 82% of reach-around climbing bouts—a style of climbing that is kinematically similar to extended-elbow vertical climbing, which most often involves the foot being semi-plantigrade on the substrate to provide propulsive force (Hunt et al., 1996)—bonobos utilized substrates nine centimeters or more in diameter (Ramos, 2014). Eastern chimpanzees have also been observed to favour small substrates when climbing unless no such substrates are available and they have no other choice than to climb larger ones (Hunt, 1992). For instance, 85% of climbing bouts observed in Mahale and Gombe chimpanzees occurred on substrates smaller than ten centimeters in diameter (Hunt, 1992). These eastern chimpanzees grasped small weight bearing substrates (<10 cm) with their foot in a power grip but generally used a plantigrade posture to set the soles of their feet against larger substrates (>10 cm) (Hunt, 1992). Similarly, Lomako bonobos grasped substrates of <20 cm in diameter with their feet in bouts of arboreal quadrupedalism, whereas their feet were plantigrade on substrates >20 cm in diameter (Susman et al., 1980). These field observations suggest that bonobos and eastern chimpanzees prefer to grasp smaller substrates with their feet in a power grip rather than place the soles of their feet against larger substrates, such as tree trunks or boughs.

Western chimpanzees do not appear to show the same preference for climbing small diameter substrates as bonobos and eastern chimpanzees. Doran (1993a, b) did not report the diameter of substrates used during climbing bouts specifically, but observed that 40.4% of all quadrumanous climbing and scrambling occurred on tree trunks (i.e., stout, primary members of the tree) (Doran, 1993a, b; Susman et al., 1980), 6.4% occurred on boughs (secondary element of

a tree 15-20 cm in diameter), 7.1% on branches (tertiary elements of a tree 2-15 cm in diameter), 33.3% on lianes (woody vines), and 12.8% on foliage (twigs and leaves growing out of branches) (Doran, 1993b). Thus, western chimpanzees used substrates >15 cm in diameter in at least 46.8% of all climbing bouts (i.e., on trunks and boughs) and substrates <10 cm (i.e., on lianes and foliage) in at least 46.1% of all climbing bouts (Table 4).

In terms of the overall time spent in trees during the day, bonobos are no more arboreal than their western and eastern chimpanzee counterparts (Ramos, 2014). It appears that the biggest difference between bonobos (LuiKotale), eastern (Mahale), and western (Tai Forest) chimpanzees is the frequency with which bonobos and western chimpanzee males climb, as they climb more frequently than eastern chimpanzees and western chimpanzee females do (Doran and Hunt, 1994; Ramos, 2014). While male western chimpanzees and male and female bonobos climb most often, western chimpanzees more frequently use larger (>15 cm) substrates such as tree trunks and boughs than bonobos and eastern chimpanzees do (Doran, 1993b), while bonobos and eastern chimpanzees prefer to use smaller substrates (<10 cm) such as small trees and vine tangles (Hunt, 1992; Ramos, 2014).

Functional morphology of the talus and medial cuneiform

The medial cuneiform forms the base of the hallux and the shape and orientation of its hallucial facet determines the degree to which the foot can grasp with the hallux (Schultz, 1930, 1934; Tocheri et al., 2011). The shape and orientation of the hallucial facet is often used to determine the degree of hallucial abduction in hominin fossils (Stern and Susman, 1983; Clarke and Tobias, 1995; Berillon, 1999; Harcourt-Smith, 2002; McHenry and Jones, 2006; Lovejoy et al., 2009). Curved hallucial facets that extend further on to the medial side of the medial

cuneiform, are angled medially, and are convex on its long axis, resulting in a more abducted set of the hallux that greatly facilitates pedal grasping (Berillon, 1999; McHenry and Jones, 2006). In contrast, modern humans and most other hominins have adducted halluxes because of relatively flat hallucial facets that are restricted to the proximal surface of the medial cuneiform (McHenry and Jones, 2006).

The talus articulates with the tibia and fibula at the talocrural joint. The relative heights of the lateral and medial trochlear rims are considered reasonable indicators of foot set in hominoids (DeSilva, 2009; Dunn et al., 2014; Knigge et al., 2015). Trochlear rims of nearly equal height orient the entire foot such that the horizontal plane of the ankle (and the plantar surface of the foot) is perpendicular to the longitudinal axis of the tibia (Harcourt-Smith and Aiello, 2004; DeSilva, 2009). A higher lateral than medial trochlear rim creates a high talar angle, which causes the entire foot to be more inverted when in resting position (i.e., the sole of the foot faces more medially). Previous work has shown that eastern gorillas have a more adducted set to their hallux combined with a more everted foot set and together these features contribute to a more terrestrially adapted foot (Schultz, 1930, 1934; Tocheri et al., 2011; Dunn et al., 2014; Knigge et al., 2015). In contrast, western lowland gorillas have a more arboreally adapted foot due to a more abducted hallucial set in combination with a more inverted foot set (Tocheri et al., 2011; Dunn et al., 2014; Knigge et al., 2015).

Objectives

In this study, three-dimensional geometric morphometric methods are used to determine whether there are functional and/or phylogenetic patterns that underlie talus and medial cuneiform shape variation among taxa in the genus *Pan*. Studies on the gorilla talus and medial

cuneiform have previously demonstrated that the shapes of these bones are strongly linked to how frequently particular populations and taxa engage in tree-climbing (Tocheri et al., 2011; Dunn et al., 2014; Knigge et al., 2015). Unlike in gorillas, the patterns of variation in talus and medial cuneiform shape among *Pan* taxa remain poorly understood, as is how these patterns might relate specifically to chimpanzee and bonobo locomotor behaviours.

Current locomotor behaviour data suggest that bonobos, western, and eastern chimpanzees do not differ from one another in degree of arboreality as much as once thought (Badrian and Badrian, 1977; Doran and Hunt, 1994; Ramos, 2014). However, these data do suggest that bonobos and eastern chimpanzees more often use smaller diameter substrates (<10 cm) when climbing, while western chimpanzees tend to climb larger diameter (>15 cm) tree trunks and boughs (Table 4). Tree-climbing constitutes the majority of arboreal locomotor activity in bonobos, western, and eastern chimpanzees (Table 3), thus climbing should have a profound effect on the morphology of the *Pan* talus and medial cuneiform. While other locomotor activities such as terrestrial knuckle-walking and perhaps even bipedality are likely to have an impact on the pedal morphology of *Pan*, variation in the width of the hallucial facet as well as in the talar angle, both respectively being well-documented indicators of pedal grasping ability and foot-set, would suggest that the morphology of these bones at least somewhat reflects variation in tree-climbing strategies. If the morphology of the talus and medial cuneiform in *Pan* does indeed reflect differences in locomotor behaviour, then these bones should show a greater emphasis on hallucial grasping in bonobos and eastern chimpanzees, and on an inverted foot set in western chimpanzees. This difference in emphasis may also be more pronounced between

bonobos and western chimpanzees, both of which appear to climb more frequently than do eastern chimpanzees (Doran and Hunt, 1994; Ramos, 2014).

The phylogenetic relationships among *Pan* likely play a role in talus and medial cuneiform shape similarities and differences. More closely related taxa should have talus and medial cuneiform shapes that are more similar to one another in comparison to more distantly related taxa. Thus, bonobos are predicted to have the most distinct talus and medial cuneiform shapes because they are more distantly related to any chimpanzee subspecies than the latter are to one another. Among subspecies, central and eastern chimpanzees are predicted to be the most similar in talus and medial cuneiform shape, followed by western and Nigeria-Cameroon chimpanzees given their known phylogenetic relationships with one another.

A final component of this study involves evaluating the talus and medial cuneiform shapes of *Pan* specimens from captive settings in the USA to explore how the shape variation in captive specimens relates to that of their wild counterparts. The objectives are to determine whether the bones of captive chimpanzee specimens resemble their wild counterparts, and whether patterns of shape variation in wild and captive specimens of known taxonomy can be used to classify captive specimens of unknown taxonomy. A previous study on the subspecies composition and founder contribution of 218 African-born captive chimpanzees in the USA found that 95% of the founders were western chimpanzees based on mitochondrial DNA (Ely et al., 2005). Although the remaining founders were comprised of eastern and central (4.6%) as well as Nigerian-Cameroon chimpanzees (0.4%), the latter disproportionately contributed to the descendant captive population while the former's contribution was significantly reduced (Ely et al., 2005). Thus, it is predicted that a majority of the captive unknown specimens from the USA

should show morphological affinities with western chimpanzees followed by Nigerian-Cameroon and then eastern and central chimpanzees.

Methods

Samples

Three-dimensional (3D) surface models of a total of 127 tali and 127 medial cuneiforms from chimpanzees and bonobos were generated from laser and CT scans. Laser scans were acquired using a NextEngine 3D Scanner HD and CT scanning used a SIEMENS Somatom Emotion CT scanner (110 kV, 70 mA, 1 mm slice thickness, 0.1 mm reconstruction increment, H50 moderately sharp kernel) (see Tocheri et al., 2011 for more details). Discrepancies between 3D models produced using different scanner types have been shown to be minimal for shape analyses like those employed in this study (Tocheri et al., 2011; Robinson and Terhune, 2017; Shearer et al., 2017; Waltenberger et al., 2021). Bones from the left side were analyzed as is and all right tali and medial cuneiforms were reflected in Meshlab (Cignoni et al., 2008) for purposes of the shape analyses.

The study sample derived mostly from adult males and females collected in the wild and was supplemented with seven older subadults (also collected in the wild and exhibiting tarsal shape that has reached adult-like proportions) and 23 captive adults. Among the captive adults, all of which derived from the USA population, 13 were wild born, one was captive born, and nine had an unknown birthplace, while taxonomically five were known to be western chimpanzees, one was an eastern chimpanzee, two were central chimpanzees, and the remaining 15 were unknown. Paired tali and medial cuneiforms from single specimens were sampled in a total of 23 western, four Nigeria-Cameroon, 30 central, and 29 eastern chimpanzees, as well as

22 bonobos, and 15 captive unknowns. An additional four tali (two central and two eastern) and four medial cuneiforms (one western, two central, and one eastern) were also sampled for individual bone analyses. Further details about the samples and the collections from which they derive are shown in Table 5.

3D geometric morphometric analysis

Using commercial software (Stratovan Checkpoint, 2018), a series of semi-landmark patches and curves were placed on the articular surfaces of these 3D models, and 3D geometric morphometric (3DGM) techniques were used to analyse the shape of each bone. The semi-landmarks used in this analysis included evenly spaced semi-landmarks on curves, surfaces, and either end of a curve (types 4, 5, and 6, respectively) (Weber and Bookstein, 2011). On each talus and medial cuneiform model, 9 x 9 patches were placed manually on the articular facets. All patches were composed of 81 semi-landmarks, including 17 moveable anchor points arranged along four sides. Four of these anchor points occurred on the corners of the patch and were placed on homologous landmark positions (see Tables 6 and 7 for descriptions). Three additional anchor points occurred along each side of every patch and were spaced evenly between corner anchor points on the outer edges of each articular facet. Finally, an anchor point occurred in the center of each patch to help position the semi-landmarks such that they were spaced as evenly as possible on the surface of each facet.

For each medial cuneiform, four patches were used with a total of 324 semi-landmarks whereas for each talus, six patches and 486 semi-landmarks were used (Tables 6 and 7, Figure 3). On the medial cuneiforms, single patches were placed on the navicular and first metatarsal (hallucial) facets. Because the intermediate cuneiform facet is almost always bipartite in *Pan*, a

third patch was placed on the second metatarsal facet combined with the distal portion of the intermediate cuneiform facet and a fourth patch was placed on the proximal portion of the intermediate cuneiform facet. For the third patch, two corner anchor points were placed on each of the two facets. The center anchor point was placed in the center of the ridge that separates the two facets along with two anchor points from the side of the patch, which were placed on either end of the ridge. On the tali, single patches were placed on the proximal calcaneal, distal calcaneal, navicular, trochlear, medial malleolar, and lateral malleolar facets.

The landmark coordinate data for each 3D model was exported in x, y, z format from Stratovan Checkpoint (2018) as .nts files and imported into R (R Core Team, 2019) for data preparation and analysis. The semi-landmarks were partitioned such that those along the outer edges of each facet were treated as curve semi-landmarks whereas those within the interior of each facet were treated as surface semi-landmarks (Bardua et al., 2019). All curve (Type 4) and surface (Type 5) semi-landmarks were slid using the criterion of minimizing bending energy (Mitteroecker and Gunz, 2013). The anchor points on the four corners of each patch were treated as the endpoints of curves (Type 6) and were not allowed to slide to prevent any Type 4 or 5 semi-landmarks from sliding off of their respective curves or surfaces (Mitteroecker and Gunz, 2013). All other anchor points and semi-landmarks were allowed to slide and projected back onto the model surface. Sliding of semi-landmarks was performed using the *slider3d()* function in the R package **Morpho** (Schlager, 2017).

The talus and medial cuneiform datasets in this study have a much higher number of variables than specimens. Discussions surrounding the possibility of spurious results in high-dimensional data like this have raised concerns over the effect of low variable to sample

size ratios (Bookstein, 2017; Cardini, 2019; Cardini, 2020a) and of sliding semilandmarks, particularly under the criterion of minimizing bending energy (Cardini, 2019), on variance-covariance structures. Small sample sizes such as the Nigeria-Cameroon chimpanzee sample in this study (n=4) are not necessarily representative of a whole population, which can lead to inaccurate mean and covariance calculations (Cardini, 2020a). Additionally, both low variable to sample size ratios and sliding of semilandmarks have been shown to alter the variance-covariance structure of isotropic normally distributed landmark data with random variation such that there is a spurious uneven distribution of variance across the first PCs (Cardini, 2019), when in reality each PC should represent a similar amount of variance. Although investigations into these issues are preliminary, it is generally agreed that strong biological signals will dampen the effect of sliding semilandmarks on spurious changes to the variance-covariance structure of shape data (Goswami et al., 2019; Cardini, 2020b).

Generalized Procrustes analysis (GPA) was performed separately on the talus and medial cuneiform after sliding the semi-landmarks using the *procSym()* function in **Morpho** (Schlager, 2017). The resulting two datasets contain the GPA superimposed coordinates representing only the talus and medial cuneiform shape variation. In GPA, variation in location, scale, and orientation among landmark configurations is removed such that only variation attributed to shape differences remains (Gower, 1975; Rohlf and Slice, 1990). Non-shape variation is removed by translating the centroids of each configuration to the origin, iteratively rotating the landmark configurations to minimize the sum of squared Euclidean distances between homologous semi-landmarks, and scaling all specimens to a unit centroid size (Slice, 2005).

Shape variation

Principal component analysis (PCA) was performed in R (R Core Team, 2019) using the *procSym()* function in **Morpho** (Schlager, 2017). Separate PCAs on the GPA superimposed coordinates (shape data) for each bone were conducted in order to visualize the distribution of specimens and their corresponding taxonomic groups within the respective shape spaces. A descriptive tool that reduces the dimensionality of multivariate data, PCA is the most common ordination method used in geometric morphometrics (Zelditch et al., 2004). Biological shape variables are always correlated because they are produced by the same developmental and genetic processes, therefore much of the variance can often be explained by a relatively small number of principal component axes (Zelditch et al., 2004).

Shape changes along the PC axes were visualized in R (R Core Team, 2019), using both 3D point clouds and warped 3D surface models. The coordinates representing -2 and +2 standard deviations on each PC were calculated using the function *pcaplot3d()* in **Morpho** (Schlager, 2017). Warped surface models and point clouds were generated by first warping the coordinates of the sample mean shape to the 3D model of the specimen closest to the sample mean in shape space using the function *warpRefMesh()* in the **geomorph** package (Adams and Otarola-Castillo, 2013). The resulting mean surface model was then warped to the coordinates of -2 and +2 standard deviations of the PC axis using the function *plotReftoTarget()* in **geomorph** (Adams and Otarola-Castillo, 2013). Point clouds representing the coordinates of -2 and +2 standard deviations of each PC axis were also generated using *plotReftoTarget()*.

Shape covariance between bones

Using 123 *Pan* specimens that had paired tali and medial cuneiforms (Table 5), a partial least squares (PLS) analysis was performed in R (R Core Team, 2019) using the function *pls2B()* in **Morpho** (Schlager, 2017) with 9999 rounds of permutation to determine whether the singular values of any latent variables were significant. This analysis performs a singular value decomposition on the cross-covariance matrix of GPA superimposed coordinates of talus and medial cuneiform specimens to identify shape patterns that maximally covary. In other words, PLS analysis helps to identify shapes in both bones that often occur together and to assess whether any combinations of shape vary between taxa. Correlation coefficients generated by the *2Bpls()* function indicate the strength of the relationship between the shapes in the medial and talus that covary in each latent variable. Shape changes along the PLS axes were visualized in R (R Core Team, 2019) as described above for the PC axes, except that the function *plsCoVar()* in **Morpho** was used (Schlager, 2017).

Shape and taxonomy

The significance of any talus or medial cuneiform shape differences among *Pan* taxa observed in the PCA and PLS analyses was tested using Procrustes ANOVA by permutation (PERMANOVA), a non-parametric multivariate technique that uses the sum of squared Procrustes distances within GPA shape space to calculate between and within-group variation from landmark data (Anderson, 2001). The PERMANOVA was performed using the function *procD.lm()* in **geomorph** (Adams and Otarola-Castillo, 2013) with 999 rounds of permutation to determine whether any of the taxonomic groups were significantly different from one another in talus or medial cuneiform shape. The Procrustes distances among the mean shapes of each taxon

were used to calculate between-group variance while the Procrustes distances between each specimen and their group mean shape were used to calculate within-group variance in each permutation (Anderson, 2001). A pseudo F-statistic—used instead of Fisher's F-statistic, which applies only to Euclidean distances—was calculated from the ratio of the between and within-group variances; lower p-values occur when the between-group variance is higher than the within-group variance (Anderson, 2001).

Post-hoc pairwise comparisons were performed using the *pairwise()* function in the **RRPP** package (Collyer and Adams, 2018, 2021) when the PERMANOVA identified a significant shape difference among the groups. The least squares group mean shape was calculated for each taxonomic group in the original, non-permuted data, and Procrustes distances were calculated between all group pairs. This procedure was repeated for each pair of taxonomic groups in each of the 999 permutations from the PERMANOVA. P-values for each pairwise comparison were based on the number of times the permutations resulted in Procrustes distances that were equal to or greater than the Procrustes distance between the original group means.

Group differences in talus and medial cuneiform shape were also explored using between-group PCA (bgPCA) and canonical variates analysis (CVA). Both bgPCA and CVA were performed in R (R Core Team, 2019) for the talus and medial cuneiform datasets separately and in combination. The bgPCAs were performed with the function *groupPCA()* and CVAs were performed with the function *CVA()* in the **Morpho** package (Schlager, 2017). Finally, using both bones together, a discriminant function analysis (DFA) was used in conjunction with the CVA to calculate the posterior probabilities of taxonomic group membership (Johnson and Wichern, 2002). For specimens with known taxonomy (the classification sample), the posterior

probabilities were calculated using resubstitution (biased) and crossvalidation (approximately unbiased) methods whereas the captive unknowns were included as an *a posteriori* testing sample only.

A bgPCA projects the principal component scores of individual specimens onto the principal component axes of the group means (i.e., the eigenvectors of the between-group covariance matrix), and like a regular PCA, involves only the rigid rotation of shape space (Boulesteix, 2005; Mitteroecker and Bookstein, 2011). The bgPCA is meant to emphasize the greatest between-group variance in a given dataset (Zelditch et al., 2004). CVA and DFA, on the other hand, also emphasize between-group differences but do so by scaling the axes to maximize the ratio of the between-group to within-group variance (Zelditch et al., 2004) such that maximum discrimination among groups is obtained (Johnson and Wichern, 2002; Mitteroecker and Bookstein, 2011).

The use of bgPCA, CVA, and DFA in 3DGM have been strongly criticized (Klingenberg and Monteiro, 2005; Bookstein, 2019; Cardini et al., 2019). For instance, spurious group separations have been identified as a pathology of bgPCAs, particularly when there is a higher number of variables in the dataset and when group sizes are highly heterogeneous, as is often the case in geometric morphometric analyses (Bookstein, 2019; Cardini et al., 2019). Similarly, CVA and DFA have strict assumptions, requiring data with invertible covariance matrices as well as homogeneous within-group covariance structures, and cannot reliably separate groups or classify unknowns unless there are many more cases than variables in the dataset (Johnson and Wichern, 2002; Mitteroecker and Bookstein, 2011). Cardini and Polly (2020) found that using leave-one-out cross validation in calculating bgPCAs greatly reduces the risk of spurious group

separation. Thus, in this study the risk of spurious group separations in the bgPCA, CVA, and DFA was mitigated by using leave-one-out cross validation (an option in the *groupPCA()* and *CVA()* functions in the **Morpho** package) and by only using 12 predictor variables: the first six PCs from the talus PCA (representing ~50% of the variance in talus shape) and the first six PCs from the medial cuneiform PCA (representing ~50% of the variance in medial cuneiform shape). The first six PCs from the talus PCA were used as the variables in the talus bgPCA and CVA, the first six PCs from the medial cuneiform PCA were used in the medial cuneiform bgPCA and CVA, and these were used as the 12 variables in the combined talus and medial cuneiform bgPCA, CVA, and DFA. Moreover, bgPCA, CVA, and DFA were not used here for explicit hypothesis testing, rather they were used solely as tools for visualization and for further exploring the results of the PCAs, PLS, and PERMANOVA to assess the morphological affinities of the captive unknown specimens.

Phylogenetic signal

The effect of the phylogenetic relationships in *Pan* on the shape variation within the data were accounted for using three analyses: Phylomorphospace analysis (PA), phylogenetically aligned component analysis (PACA), and phylogenetic PCA (Phy-PCA). It is important to determine the effect that phylogenetic relationships have on the shape variation of the talus and medial cuneiform in chimpanzee subspecies and bonobos because these taxa are so closely related. A phylogenetic tree was generated in R by the *read.tree()* function in the **ape** package (Paradis and Schliep, 2019) using the divergence dates in Figure 2. The *gm.prcomp()* function in **geomorph** was used to create a phylogenetic covariance matrix from the phylogenetic tree, and then generated PAs, PACAs, and Phy-PCAs for the talus and medial cuneiform data separately

(Collyer and Adams, 2018, 2020). Phylogenetic analyses are generally conducted on species and subspecies data, therefore group mean shapes were calculated for the talus and medial cuneiform of each taxonomic group and the three analyses were performed on these group means. The function *physignal()* in **geomorph** was used to determine the strength of the phylogenetic signal by generating multivariate K (Kmult) values for the separate talus and medial cuneiform datasets and univariate K (Kuni) values for each component of each analysis, as well as determine the significance of the multivariate K value in the separate talus and medial cuneiform datasets (Collyer and Adams, 2018, 2020).

Phylogenetic signal describes the commonly observed pattern where closely-related species have more similar traits to one another than to less-related taxa (Bloomberg et al., 2003). The K statistic reflects the degree to which traits differ in taxa in comparison to what is expected under Brownian Motion (Adams, 2014). Under Brownian Motion taxa are predicted to accumulate a proportionate number of trait differences to the amount of time since their divergence from one another (Revell, 2009). K values less than 1 indicate that there are more trait differences between taxa than expected under Brownian Motion, K values of 1 indicate random trait evolution, which follows the pattern of changes predicted by Brownian Motion, and K values greater than 1 indicate that closely related taxa are more similar to one another than predicted under Brownian Motion (Adams, 2014).

Used together, PA, PACA, and Phy-PCA allow us to evaluate the morphological patterns associated with or independent of evolutionary relationships and determine how each contributes to the patterns of shape variation in the dataset. PA involves a rotation of the data space around its ordinary least squares (OLS) centered mean, revealing the maximum variance in the data on

the first principal component (Collyer and Adams, 2020). The distribution of points on the principal components of a PA are the same as they would be in a PCA of group means, however, a PA also involves the projection of the phylogenetic tree edges onto the group means principal components (Collyer and Adams, 2020). Univariate K values for each component of the PA reflect the degree to which variance in the talus or medial cuneiform shape data can be predicted by the phylogenetic relationships within *Pan*. PACA is a method introduced by Collyer and Adams (2020) to be used together with Phy-PCA and PA. Like a PLS analysis, the PACA involves a singular value decomposition of the cross-product of the covariance matrix of GPA superimposed coordinates of talus or medial cuneiform specimens and the phylogenetic covariance matrix (Collyer and Adams, 2020). The first few components of a PACA are expected to strongly covary with the phylogenetic covariance matrix, as the PACA aligns the shape data to the phylogenetic signal (Collyer and Adams, 2020). The shape change in the first few components of the PACA represent the shape differences that covary most with the phylogenetic signal. Phy-PCA is similar to PA in that it involves a rotation of the data space around its general least squares (GLS) centered mean, however, in this method the data representing the greatest variation that carries the least phylogenetic signal is projected onto the first principal component (Collyer and Adams, 2020). Shape changes in the articular surfaces of the talus and medial cuneiform that were predicted to show functional differences between taxa (i.e. the talar trochlea and the hallucial facet) were visualized as point clouds along the first two axes of the PACAs and the Phy-PCAs using *plotRefToTarget()* (Collyer and Adams, 2018, 2020).

Results

Shape variation

The talus PCA resulted in considerable amounts of overlap between the five closely related taxonomic groups on all PCs and the total variance was distributed fairly evenly across multiple PCs. For instance, PCs 1 thru 6 explained 13.8%, 8.3%, 7.4%, 6.6%, 5.4%, and 4.7% of the variance, respectively, and it was not until PC22 that the proportion of variance explained dropped below 1% (Table 8). The best separation among taxonomic groups was observed on PC1 and 4, which together explained 20.4% of the total shape variance (Figure 4). Western chimpanzees and the captive unknowns cluster positively along PC1 because they have slightly higher lateral relative to the medial trochlear rims, and distal calcaneal facets that are truncated on the medial side of the talar head. In contrast, the tali of some central and eastern chimpanzees as well as many bonobos on the negative side of PC1 have relatively lower lateral trochlear rims, and the distal end of the distal calcaneal facets extends medially across the entire plantar surface of the talar head. Bonobos cluster more negatively along PC4 because they have flatter proximal calcaneal facets whereas eastern and some central chimpanzees cluster more positively on this axis because they have more concave proximal calcaneal facets.

The medial cuneiform PCA also resulted in considerable amounts of overlap between taxonomic groups with the total variance distributed fairly evenly across multiple PCs. In this case, PCs 1 thru 6 explained 14.5%, 13.0%, 9.5%, 7.3%, 6.5%, and 4.2% of the variance, respectively, and it was not until PC21 that the proportion of variance explained dropped below 1% (Table 8). The best group separations among taxonomic groups were observed on PC1 and 2, which together explain 27.5% of the total variance and almost completely separate bonobos from

western chimpanzees and captive unknowns (Figure 5). Bonobos cluster negatively along PC1 because they have wider hallucial facets that extend further onto the medial side of the bone, and positively along PC2 because the proximal portion of their intermediate cuneiform facets is pushed inferolaterally and their navicular facets are narrower dorsoplantarly. In contrast, western chimpanzees and the captive unknowns cluster positively along PC1 because they have narrower hallucial facets that do not extend as far onto the medial side, and negatively along PC2 because the proximal portion of their intermediate cuneiform facet occupies the entire length of the border with the navicular facet, along with dorsoplantarly wider navicular facets.

Shape covariance between bones

The first latent variable in the PLS analysis explained 42.7% of the total covariance between the talus and medial cuneiform shapes, had a correlation coefficient of 0.67, and a p-value of 0.0001 (Figure 6). The first latent variable separated bonobos almost completely from western chimpanzees, while Nigeria-Cameroon, eastern, and central chimpanzees fell in between these two extremes. Western chimpanzees and the captive unknowns cluster at the negative ends of both axes, whereas bonobos cluster at the positive ends of both axes. On the negative end of the medial cuneiform axis, these bones have narrower hallucial facets, dorsoplantarly wider navicular facets, and proximodistally narrower proximal portions of the intermediate cuneiform facet. Medial cuneiforms with these features covary with tali that have relatively higher lateral than medial trochlear rims, more concave proximal calcaneal facets, and distal calcaneal facets that are truncated on the medial side of the talar head. At the positive end of the medial cuneiform axis, these bones have wider hallucial facets, dorsoplantarly narrower navicular facets, and wider proximal portions of the intermediate cuneiform facet. These medial cuneiforms

covary with tali that have medial and lateral trochlear rims that are similar in height, flatter proximal calcaneal facets, and distal calcaneal facets that span the entire plantar surface of the talar head. Finally, Figure 7 shows how the captive specimens compare with their wild counterparts in the PLS analysis. Five of the six captive specimens for which their subspecies is known group within the ranges of their taxonomic groups while a single captive central chimpanzee specimen falls just outside the negative range of wild central chimpanzees. All of the captive specimens for which their taxonomy is unknown cluster negatively along both axes with wild western chimpanzees as does the only western chimpanzee specimen included that is known to have been born in captivity.

Shape and taxonomy

Talus The PERMANOVA of talus shape indicated that at least two taxa were significantly different from one another ($p = .001$). Post-hoc pairwise comparisons of the Procrustes distances between pairs of group mean shapes revealed several significant differences between taxa using a Bonferroni correction for multiple comparisons ($p < .005$) (Table 9). Bonobos were significantly different from all other taxa ($p = .001$) except Nigeria-Cameroon chimpanzees ($p = .008$) while western chimpanzees were also significantly different from central ($p = .001$) and eastern ($p = .001$) but not from Nigeria-Cameroon chimpanzees. Eastern and central chimpanzees were also significantly different from each other ($p = .003$) but not from Nigeria-Cameroon chimpanzees. In the bgPCA (Figure 8), bonobo and to a lesser extent western chimpanzee tali separated from eastern and to a lesser extent central chimpanzees along bgPC1 while Nigeria-Cameroon chimpanzees fell in between western chimpanzees and central and eastern chimpanzees. Bonobos clustered negatively away from all chimpanzee subspecies along bgPC2. In the CVA

(Figure 9), bonobos clustered away from all other taxa along CAN1 while CAN2 mostly separated western from central chimpanzees.

Medial cuneiform The PERMANOVA of medial cuneiform shape indicated that at least two taxa were significantly different from one another ($p = .001$). Post-hoc pairwise comparisons of group mean shapes using a Bonferroni correction for multiple comparisons ($p < .005$) yielded significant differences between all pairs ($p < .002$) with four exceptions: Nigeria-Cameroon chimpanzees compared to central, eastern, and western chimpanzees; and central compared to eastern chimpanzees (Table 10). In the bgPCA (Figure 10), bonobo medial cuneiforms separated from those of Nigeria-Cameroon and western chimpanzees along bgPC1 as well as from those of central and eastern chimpanzees to a lesser extent. In the CVA (Figure 11), CAN1 separated western chimpanzees from bonobos with Nigeria-Cameroon, central, and eastern chimpanzees falling in between. No group separation occurred along bgPC2 or CAN2.

Both bones The first six PCs from the talus PCA (representing ~50% of the variance in talus shape) and the first six PCs from the medial cuneiform PCA (representing ~50% of the variance in medial cuneiform shape) were used as predictor variables in several additional exploratory multivariate analyses. In the bgPCA, bonobos separated completely from western chimpanzees, and from eastern, central, and Nigeria-Cameroon chimpanzees to a lesser extent along bgPC1, whereas along bgPC2, eastern and central chimpanzees separated almost completely from bonobos and western chimpanzees (Figure 12). In the CVA, group separation on CAN1 was similar to that of bgPC1, separating bonobos from western, eastern, Nigeria-Cameroon, and, to a lesser extent, central chimpanzees (Figure 13). On CAN2, eastern and, to a lesser extent, central, and Nigeria-Cameroon chimpanzees separated from western

chimpanzees.

In a DFA, resubstitution successfully classified 100% of bonobos and Nigeria-Cameroon chimpanzees, and 91%, 75%, and 68% of western, eastern, and central chimpanzees, respectively. In contrast, crossvalidation successfully classified 90.9% of bonobos, 83% of western, 54% of eastern, 52% of central, and 50% of Nigeria-Cameroon chimpanzees. Using the 15 captive unknowns as a testing sample, 12 specimens were classified as western chimpanzees with an average posterior probability of 95%, one each was classified as a central, eastern, and Nigeria-Cameroon chimpanzee with respective posterior probabilities of 71%, 65%, and 61%.

Phylogenetic signal

Talus The talus dataset had a weak phylogenetic signal, with a significant ($p=0.018$) multivariate K value of 0.52.

The first PC of the talus PA had a strong phylogenetic signal while the second PC had a weak signal (Figure 14). PC1 represented 42.5% of the variance with a univariate K value of 1.55, PC2 represented 27.8% with a univariate K value of 0.45, and PCs three to five together represent 29.7% of the variance. PC1 separated bonobos on the negative end of the axis from all chimpanzees, with western and Nigeria-Cameroon chimpanzees falling furthest toward the positive end of the axis. PC2 separated western chimpanzees and bonobos on the negative end from eastern, central, and Nigeria-Cameroon chimpanzees on the positive end.

Component one of the talus PACA represented 82.6% of the covariance between the shape data and the phylogenetic covariance matrix and had a univariate K value of 1.73 (Figure 15). Component two represented 13.9% with a univariate K value of 0.50, and components three to five combined represented very little covariance (<2.84%). Component one separated bonobos

on the negative end from all chimpanzees on the positive end. Visualization of shape change in the angle of the talar trochlea showed that chimpanzees have higher lateral trochlear rims while bonobo trochlear rims are more even in height. Component two separated western and Nigeria-Cameroon chimpanzees from eastern and central chimpanzees. Shape visualization showed that western and Nigeria-Cameroon chimpanzees fell on the positive end in part because they have higher lateral and lower medial trochlear rims as opposed to more even trochlear rims in eastern and central chimpanzees.

All components of the talus Phy-PCA had weak phylogenetic signals (Figure 16). PC1 represented 49.0% of the total variance with a univariate K value of 0.24, PC2 represented 29.1% with a univariate K value of 0.21, and PCs three to five together represented <22.0% variance. PC1 separated western chimpanzees on the positive end from all other taxa with Nigeria-Cameroon chimpanzees falling furthest to the negative end. PC2 separated eastern chimpanzees on the negative end from all other taxa. There was no obvious difference in the angle of the talar trochlea, although groups on the positive end PC2 appeared to have slightly higher lateral than medial trochlear rims than on the negative ends of these axes.

Medial cuneiform The medial cuneiform dataset had a weak phylogenetic signal, with a significant (p=0.022) multivariate K value of 0.55.

The first PC of the medial cuneiform PA had a strong phylogenetic signal (Figure 17). PC1 represented 51.3% of the variance with a univariate K value of 1.04, PC2 represented 30.9% with a univariate K value of 0.31, and PCs three to five together represented <17.8% of the variance. PC1 separated bonobos on the negative end from the chimpanzees on the positive end with Nigeria-Cameroon chimpanzees furthest toward the positive end of the axis. PC2 separated

bonobos and Nigeria-Cameroon chimpanzees on the negative end from western and to a lesser extent eastern and central chimpanzees on the positive end.

Component one of the medial cuneiform PACA represented 88.3% of the covariance between the shape data and the phylogenetic covariance matrix and had a univariate K value of 2.12, component two represented 8.41% with a univariate K value of 0.57 (Figure 18), and components three to five represented very little covariance (<3.1%). Component 1 separated bonobos on the positive end due to a wider and more medially extended hallucial facet from the chimpanzees on the negative end. PC2 separated Nigeria-Cameroon chimpanzees on the positive end from eastern and central chimpanzees on the negative end, with no obvious differences in the width or extension of the hallucial facet.

All components of the medial cuneiform Phy-PCA contained weak phylogenetic signals (Figure 19). PC1 represented 68.8% of the variance with a univariate K value of 0.26, PC2 represented 15.1% with a univariate K value of 1.55, and PCs three to five together represented <16.3% variance. PC1 separated Nigeria-Cameroon chimpanzees on the positive end from the other taxa on the negative end, with no differences in the hallucial facet. PC2 separated bonobos on the negative end due to a wider and more medially extended hallucial facet from western and Nigeria-Cameroon chimpanzees on the positive end, with eastern and central chimpanzees in the middle.

Discussion

Shape variation, function, and phylogeny

This study aimed to explore talus and medial cuneiform shapes among taxa in *Pan* and to determine whether and to what extent any shape variation may be related to differences in

locomotor behaviour. Based on previous field studies of locomotor behaviour (Hunt, 1992; Doran and Hunt, 1994; Ramos, 2014) (Table 4), bonobos and eastern chimpanzees were predicted to have medial cuneiform morphology that emphasizes hallucial grasping because these taxa more often use smaller diameter (<10 cm) substrates when climbing. In contrast, western chimpanzees were predicted to have talus morphology that emphasizes a more inverted foot set because no such preference for smaller diameter substrates during climbing has yet been documented for this taxon, and instead they are known to more frequently climb larger diameter (>15 cm) tree trunks and boughs (Doran, 1993b). Phylogenetic relationships among *Pan* were also predicted to play an important role in determining the shapes of the talus and medial cuneiform, with more closely related taxa having more similar morphology to one another than to more distantly related taxa.

In the 3DGM analyses, the PCAs for each bone revealed some subtle differences in talus and medial cuneiform shape among *Pan* taxa (Figures 4 and 5). These morphological subtleties were brought into clearer focus by the covariance of features between both tarsal bones in the PLS analysis (Figure 6), which separated bonobos nearly completely from western chimpanzees, with eastern, central, and to a lesser extent, Nigeria-Cameroon chimpanzees, falling in between these two extremes. In comparison to other *Pan* taxa, western chimpanzees have narrower hallucial facets, dorsoplantarly wider navicular facets, and proximodistally narrower proximal portions of the intermediate cuneiform facet. Their tali have higher lateral trochlear rims and more strongly curved proximal calcaneal facets, as well as distal calcaneal facets that are truncated on the medial side of the talar head. In contrast, bonobos are characterized by medial cuneiforms with very wide hallucial facets that extend further onto the medial surface of the

bone, dorsoplantarly narrower navicular facets, and wider proximal portions of the intermediate cuneiform facet when compared with other *Pan* taxa, especially western chimpanzees. Bonobo tali also have comparatively more even lateral and medial trochlear rims, weakly concave proximal calcaneal facets, and distal calcaneal facets that span the entire plantar surface of the talar head.

The shapes of the bonobo talus and medial cuneiform appear to covary as a functional unit that emphasizes hallucial grasping at the first tarsometatarsal joint but not inversion at the talocrural joint. For bonobos, who strongly favour smaller diameter substrates when climbing (Ramos, 2014), greater hallucial abduction likely facilitates pedal grasping and confers greater stability when climbing on branches, lianes (woody vines), and foliage (twigs and leaves growing out of branches). The exact opposite pattern was observed in western chimpanzees, which have higher lateral trochlear rims that emphasize inversion at the ankle joint but not hallucial grasping. For western chimpanzees, who favour larger diameter substrates when climbing (Doran, 1993b), a more inverted foot set likely facilitates the plantigrade placement of the soles of their feet directly against climbing substrates, helping to keep the center of mass as close to the substrate as possible, and decreasing the risk of falling (DeSilva, 2009; Knigge et al., 2015). Overall, the methods employed in this study extracted patterns of morphological variation that are consistent with differences in the locomotor behaviours observed in chimpanzees and bonobos.

The low genetic diversity within western chimpanzees in comparison to other chimpanzees (Fischer et al., 2011), might help to explain their distinct combination of talus and medial cuneiform shapes. In fact, bonobos and western chimpanzees have some of the lowest

genetic diversity of all the great apes, and the bonobo genome has the same pattern of heterozygosity as in the genomes of modern human populations that have experienced extreme genetic bottlenecks (Prado-Martinez et al., 2013). Western chimpanzees appear to have experienced a recent genetic bottleneck from which they recovered within the current interglacial (Lester et al., 2021). Although all chimpanzees and bonobos are terrestrial knuckle walkers and highly proficient climbers, selective pressures may have acted more readily on the small, isolated ancestral populations of bonobos and western chimpanzees, resulting in the respective morphological specializations of these taxa documented in this study.

Both PACA and Phy-PCA were used to determine whether or not shape changes associated with differing styles of climbing in the *Pan* talus and medial cuneiform coincide with the phylogenetic signal in the shape data. In other words, these analyses were used to determine whether or not the shape differences that emphasize pedal grasping in bonobos and an inverted foot set in western chimpanzees have evolved as a result of the phylogenetic relationships between taxa (i.e., according to a Brownian Motion model of evolution) or as a result of factors other than phylogeny (Collyer and Adams, 2020). Along all PACA and Phy-PCA components, none showed K values equal or especially close to 1, suggesting that the amounts of shape change observed are either less than or more than expected under a Brownian Motion model of evolution (Figures 15, 16, 18, 19). Overall, these results suggest that the shapes of the medial cuneiform and talus (including features related to the hallucial facet and the talar angle) have both evolved more shape change than is predicted by the phylogeny, as indicated by the multivariate K values of about 0.5 for both bones and the low univariate K values for many components.

The phylogenetic relationships among *Pan* were nevertheless predicted to have an impact on the similarities of talus and medial cuneiform shape between closely related taxa. Despite the weak overall phylogenetic signal in the entire talus and medial cuneiform datasets, a strong phylogenetic signal was detected in PC1 of the PA and in component one of the PACA for both the talus and medial cuneiform, all of which separated the bonobo group mean shapes from chimpanzee group means (Figures 14, 15, 17, 18). In both PAs, eastern and central chimpanzees were shown to be the most similar in group mean talus and medial cuneiform shape as predicted by their close phylogenetic relationship (Prado-Marinez et al., 2013; Lobon et al., 2016; deManuel et al., 2016). Eastern and central chimpanzees also clustered together consistently in other analyses due to their shared patterns of covariance in talus and medial cuneiform shape (Figure 6), the shapes of these bones individually (Figures 4 and 5), their group mean shapes (Figures 8–11), and the combined shapes of both bones (Figures 12 and 13).

These closely related taxa have a more generalized talus and medial cuneiform morphology that is, generally, intermediate between that of bonobos and western chimpanzees and that does not appear to emphasize hallucial grasping over an inverted foot set or vice versa. For eastern chimpanzees, this result was somewhat unexpected given that they also show a preference for climbing using small diameter substrates (<10 cm), like bonobos do. However, eastern chimpanzees are known to climb less often overall in comparison to either bonobos or western chimpanzees (Doran and Hunt, 1994; Ramos, 2014). Although some eastern chimpanzees did have relatively wide hallucial facets, medial cuneiform shape was otherwise much more variable among eastern chimpanzees than it was among bonobos (Figure 5). Eastern and central chimpanzees were significantly different in mean talus shape (Table 9) but nearly

indistinguishable from one another in mean medial cuneiform shape (Table 10). The similarities observed between central and eastern chimpanzees probably reflects their relatively recent genetic divergence from one another (~0.15 Ma) (Prado-Martinez et al., 2013; Lobon et al., 2016; de Manuel et al., 2016) and their overall genetic similarities, which have been used previously to suggest that they should be treated as a single subspecies (Gonder et al., 2011).

Nigeria-Cameroon chimpanzees are more closely related to western chimpanzees than to any other chimpanzees (Prado-Martinez et al., 2013; Lobon et al., 2016; deManuel et al., 2016). Three of the Nigeria-Cameroon specimens showed a similar combination of talus and medial cuneiform shape features as in western chimpanzees (Figure 6), a result consistent with the relatively recent divergence time for these taxa (~0.25 Ma) (de Manuel et al., 2016), although one specimen grouped with bonobos and central and eastern chimpanzees in the PLS analysis. Nigeria-Cameroon and western chimpanzees group further apart from one another than central and eastern chimpanzees in both PAs (Figures 14 and 17), in the medial cuneiform PACA (Figure 18), and in both Phy-PCAs (Figures 16 and 19). This may be accounted for in part by the fact that more time has elapsed since the divergence of western and Nigeria-Cameroon chimpanzees than eastern and central chimpanzees (Lobon et al., 2016; deManuel et al., 2016). Additionally, there has been very little admixture between western and other chimpanzee taxa, whereas there has been some ancient gene flow between eastern, central, and Nigeria-Cameroon chimpanzees and even more ancient admixture between these three taxa and bonobos (Mitchell et al., 2015; deManuel et al., 2016). Finally, the small sample size of Nigeria-Cameroon chimpanzees (n=4) very likely played a role in the separation between them and western

chimpanzees in the PAs and the Phy-PCAs as this sample is not likely to be representative of the entire variation across the subspecies.

The small Nigeria-Cameroon chimpanzee sample almost certainly contributed to a lack of statistical power for post-hoc pairwise tests, which indicated that their talus was similar in shape to that of all other chimpanzees and bonobos (Table 9), while their medial cuneiform was only significantly different in shape from that of bonobos (Table 10). The range of shape variation observed within this small Nigeria-Cameroon sample in the PLS analysis, in combination with the unexpected dissimilarity with western chimpanzees in the PAs, the medial cuneiform PACA and both Phy-PCAs, suggest that Nigeria-Cameroon chimpanzees have a more generalized morphology than western chimpanzees, similar to what was observed in eastern and central chimpanzees. Further investigation into the shape of the Nigeria-Cameroon chimpanzee talus and medial cuneiform would benefit from a larger sample size. Field studies of Nigeria-Cameroon and central chimpanzee locomotor behaviour are also required to determine whether they climb more similarly to western chimpanzees or to eastern chimpanzees.

Safe climbing is thought to be one of the main selective pressures shaping bonobo and chimpanzee anatomy (Pontzer and Wrangham, 2004). Obviously, these species are all excellent climbers, but the results of this study suggest that their talus and medial cuneiform shapes are distributed along a morphocline that is reasonably related to the variable use of substrates of different size during climbing and the frequencies of climbing behaviours overall. Eastern, central, and possibly Nigeria-Cameroon chimpanzees have a combination of talus and medial cuneiform shapes that do not necessarily emphasize pedal grasping or foot inversion at the expense of the other. In this respect, their shape patterns are somewhat generalized, lacking any

specific specializations for substrate size preferences during climbing. Bonobos and western chimpanzees, however, display more specialized shape features that emphasize habitual pedal grasping conferring greater stability on smaller substrates in the former and plantigrade postures that help reduce the risk of falls while climbing larger substrates in the latter.

Captive Chimpanzees

A second objective of this study was to evaluate the talus and medial cuneiform shapes of *Pan* specimens from captive settings in the USA to explore how their shape variation compares to that of their wild counterparts. The taxonomy of some of the captive chimpanzees used in this study was known, including five western, one eastern, and two central chimpanzees. One of these specimens, a western chimpanzee, was born in captivity whereas the rest were wild born. Each of these eight captive specimens grouped within or relatively near to their subspecies clusters along each PC and in the PLS analysis (Figures 4, 5, 7) and did not appear to differ substantially from their wild counterparts in the patterns of shape variation observed in this study. In other words, there was no clear observable difference between chimpanzees that lived their entire lives in the wild compared with those that lived a majority of their lives in captivity. Additionally, the one captive-born western chimpanzee did not show any noticeable shape differences from other western chimpanzees on any PCs or in the PLS analysis (Figures 4, 5, 7).

Another fifteen captive specimens examined were of unknown taxonomy. Based on the posterior probabilities of group membership of the DFA, 12 of these captive unknowns were classified as western chimpanzees and one each was classified as a central, eastern, and Nigeria-Cameroon chimpanzee (Figure 13). In the PLS analysis, two captive unknowns that were classified as western chimpanzees fall just to the negative side of the wild and captive western

chimpanzee cluster, while one other falls to the extreme negative end of the medial cuneiform axis (Figure 7). The latter specimen was obtained from a biomedical supply company, and its extreme medial cuneiform shape may be the result of living in a vastly different environment than is typical for wild or captive chimpanzees. In the PLS analysis, the captive unknown classified as an eastern chimpanzee fell within the range of its wild counterparts, and the captive unknowns classified as a central and a Nigeria-Cameroon chimpanzee fell just outside of their respective subspecies' clusters (Figure 7).

These results are consistent with previous genetic work that showed that the vast majority (95%) of the founders of the USA captive chimpanzee population were western chimpanzees (Ely et al., 2005). Overall, captivity seems to have played only a minor role in the shape patterns of the *Pan troglodytes* talus and medial cuneiform observed in this study. This suggests that there may be limited potential for phenotypic plasticity, or changes in phenotype caused by environmental or behavioural factors throughout an individual's lifetime, in the talar angle of the talus and the hallucial facet of the medial cuneiform in chimpanzees. Similar results have also been reported for gorilla tali, scapulae, long bone lengths, and articular sizes (Bello-Hellegouarch et al., 2013; Ruff et al., 2013; Venkataraman et al., 2013; Dunn et al., 2014). Although further investigation including a much larger captive sample size is required, it may be that the patterns of covariance observed here in the talus and medial cuneiform are under reasonably tight genetic control.

Conclusion

Bonobos and western chimpanzees are two closely-related taxa that appear to have evolved specialized talus and medial cuneiform shapes in relation to those of eastern and central

chimpanzees. These specialized features likely relate to documented differences among these taxa in preferences for climbing on substrates of different sizes (Doran, 1993b; Ramos, 2014). If true, these specializations and climbing preferences may have evolved due to selective pressures in combination with genetic bottlenecks in ancient western chimpanzee populations within the last 600 thousand years and bonobo populations during the past 1 to 2 million years. As comparable changes have also been documented in gorillas (Tocheri et al., 2011; Dunn et al., 2014; Knigge et al., 2015), it is also possible that relatively subtle changes in the morphology of these and other tarsal bones may have evolved over the course of hominin evolution as well, especially in taxa that included arboreality as an important part of their locomotor and/or other behavioural repertoires (Richmond, 2001; Thorpe et al., 2007; Lovejoy et al., 2009).

The results of this study suggest that in the *Pan* tarsus the talus and medial cuneiform covary as a functional unit. In bonobos, the medial cuneiform emphasizes hallucial grasping but not inversion at the talocrural joint. In western chimpanzees, the talus emphasizes an inverted foot set but not hallucial grasping. Eastern, central, and possibly Nigeria-Cameroon chimpanzee talus and medial cuneiform shapes fall in between these two extremes. Interestingly, the pattern of covariance observed in this study among chimpanzees and bonobos does not exist in modern humans. Modern humans have a non-grasping hallux due to a relatively flat hallucial facet on the medial cuneiform that lacks any medial extension and is instead oriented distally (McHenry and Jones, 2006). However, modern humans are unable to invert their ankle to the same degree as chimpanzees without severe injury (DeSilva, 2009), in large part due to a talocrural joint that results in an everted foot set in neutral position. In this respect, modern human medial cuneiforms are most similar to those of western chimpanzees whereas modern human tali most

closely resemble those of bonobos. If the pattern of covariance observed in *Pan* also characterized the *Pan-Homo* ancestor, then this pattern must have become dissociated at some point during early hominin evolution in order to produce the combination seen in modern humans (i.e., an everted foot set combined with an adducted hallux).

Figures

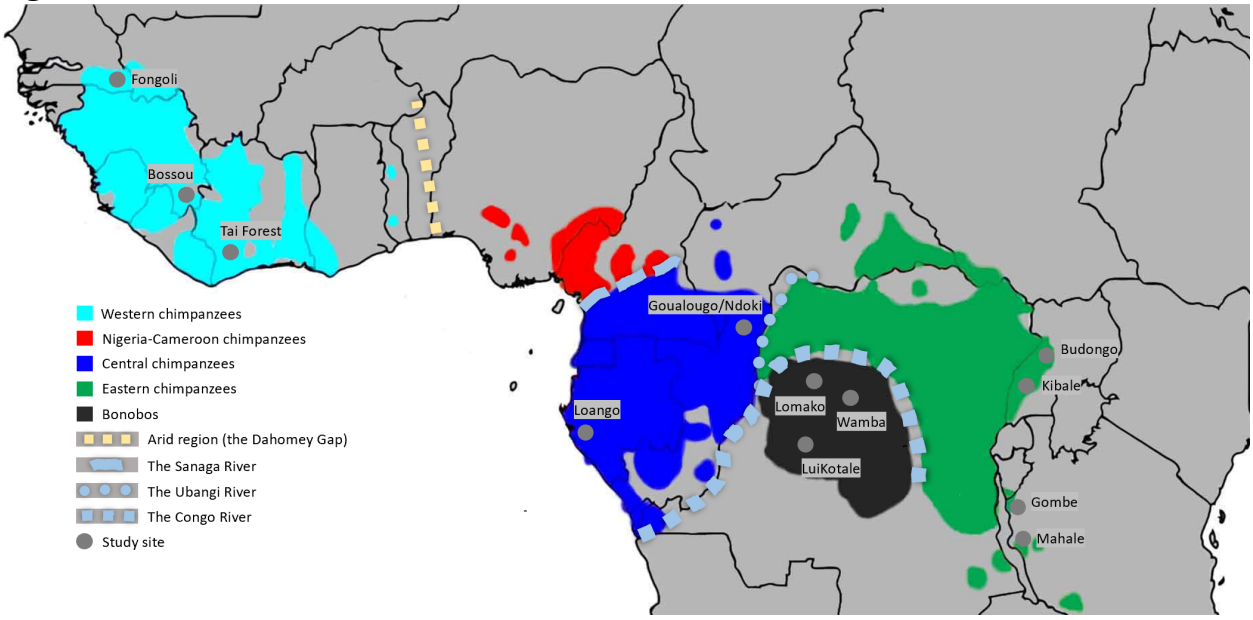

Figure 1. Distribution of *Pan* across central Africa and the geographic barriers separating each taxon. Grey circles show the locations of major long-term study sites. Modified from Lobon et al., 2016. (RETURN TO TEXT)

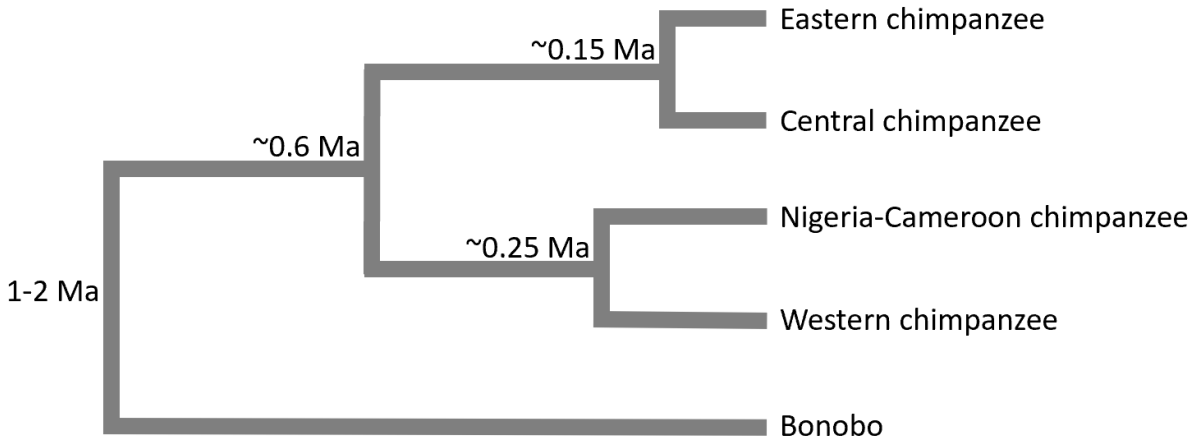

Figure 2. Phylogenetic relationships among chimpanzees and bonobos and estimated divergence dates in millions of years (Ma). Modified from de Manuel et al., 2016. (RETURN TO TEXT)

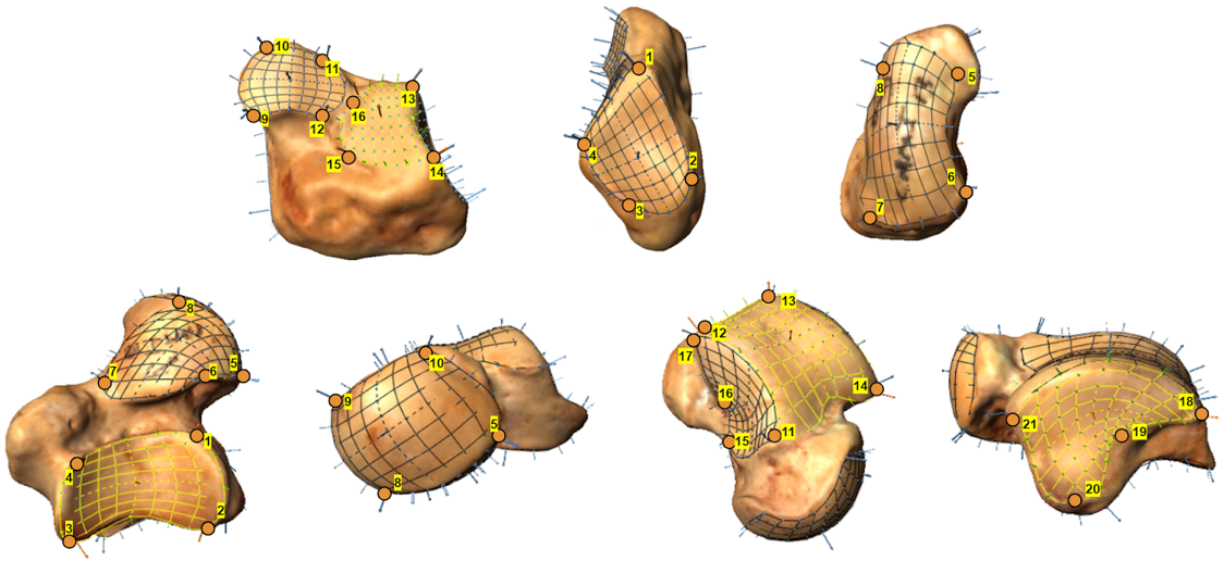

Figure 3. The 9 x 9 semi-landmark patches and anchor points on the articular facets of a *Pan troglodytes troglodytes* (PCM-cam-i-13) medial cuneiform (top row; from left to right are the lateral, proximal, and distal views) and talus (bottom row; from left to right are the plantar, proximal, dorsal, and lateral views). The numbered orange dots on the four corners of each patch show the anchor points (see Tables 5 and 6), which coincide with a set of the landmarks modified from Harcourt-Smith, 2002. (RETURN TO TEXT)

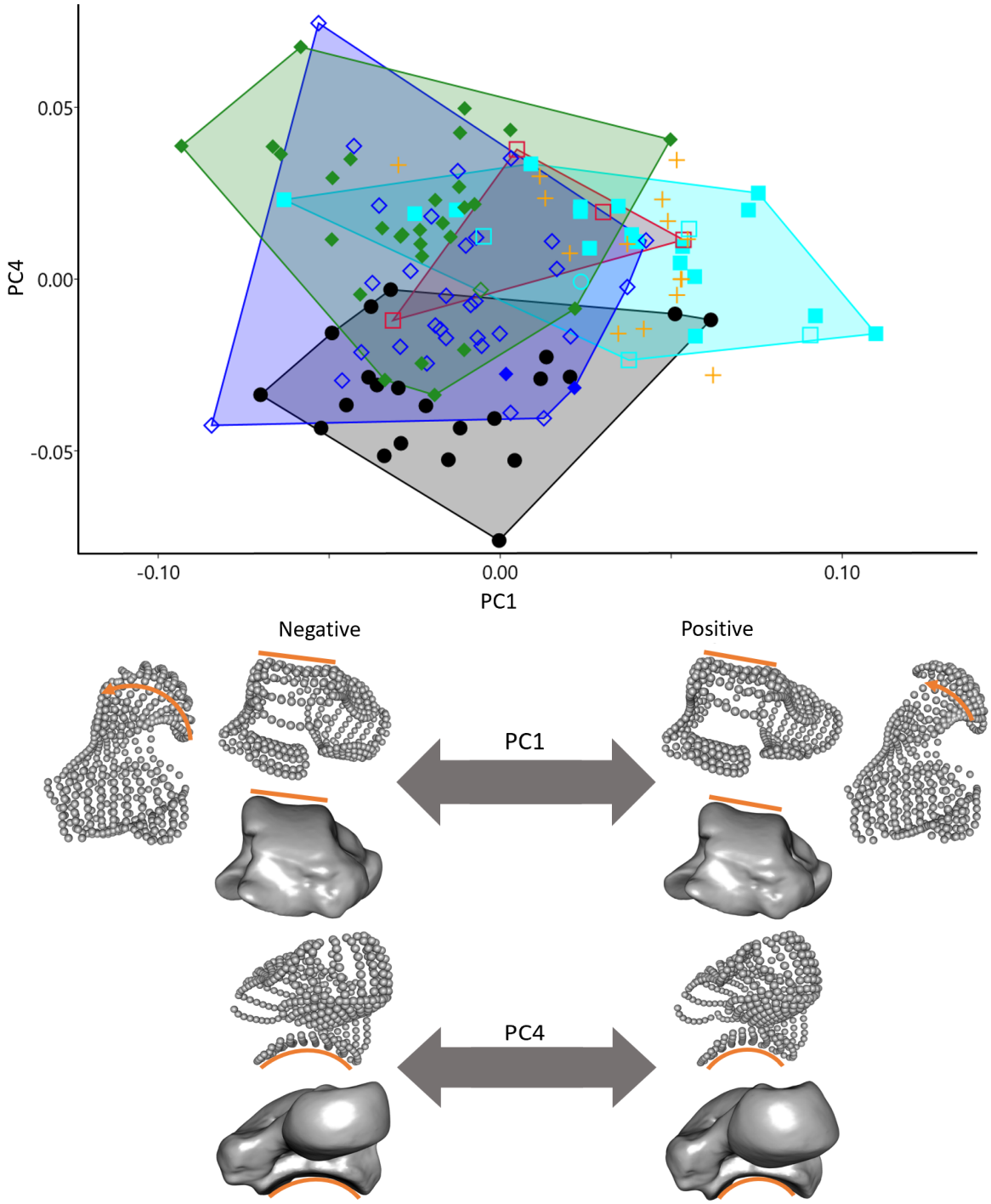

Figure 4. Plot of the principal components (PC1 and PC4) generated from the talus shape data. PC1 accounts for 13.8% of the variation, PC4 accounts for 6.6% (bonobos, black solid circles; western chimpanzees, light blue solid squares; Nigeria-Cameroon chimpanzees, red open squares; central chimpanzees, dark blue open diamonds; eastern chimpanzees, green solid diamonds; captive western, light blue open squares; captive-born western, light blue open circle; captive central, dark blue solid diamond; captive eastern, green open diamond; captive unknowns, orange crosses). (RETURN TO TEXT)

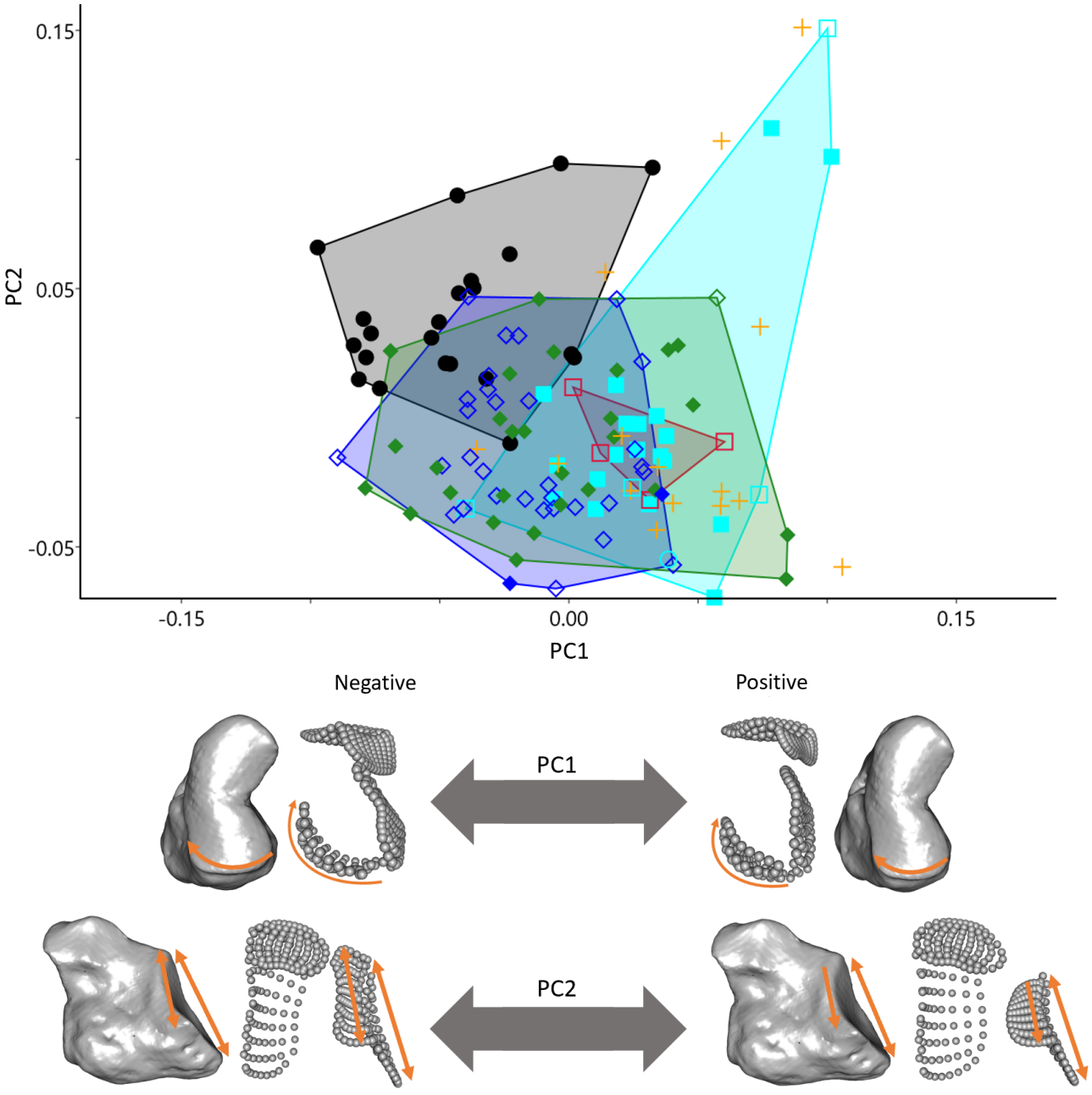

Figure 5. Plot of the principal components (PC1 and PC2) generated from the medial cuneiform shape data. PC1 accounts for 14.5% of the variation, PC2 accounts for 13.0% (symbols as in Fig. 4). (RETURN TO TEXT)

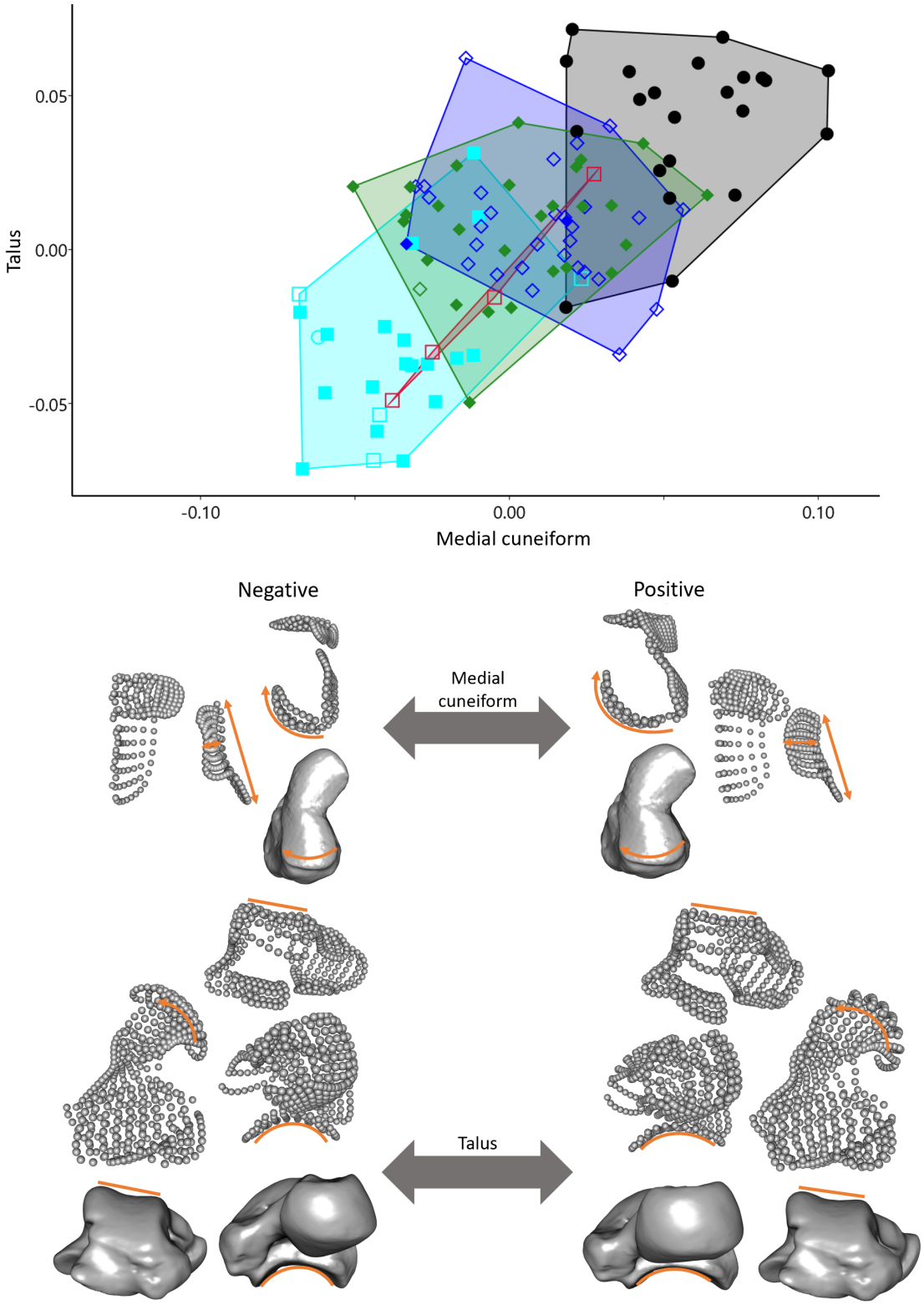

Figure 6. Plot of the PLS analysis generated from the medial cuneiform and talus shape data and accounting for 46% of the total covariance between bones with a correlation coefficient of 0.67 and a p-value of 0.0001 (symbols as in Fig. 4). (RETURN TO TEXT)

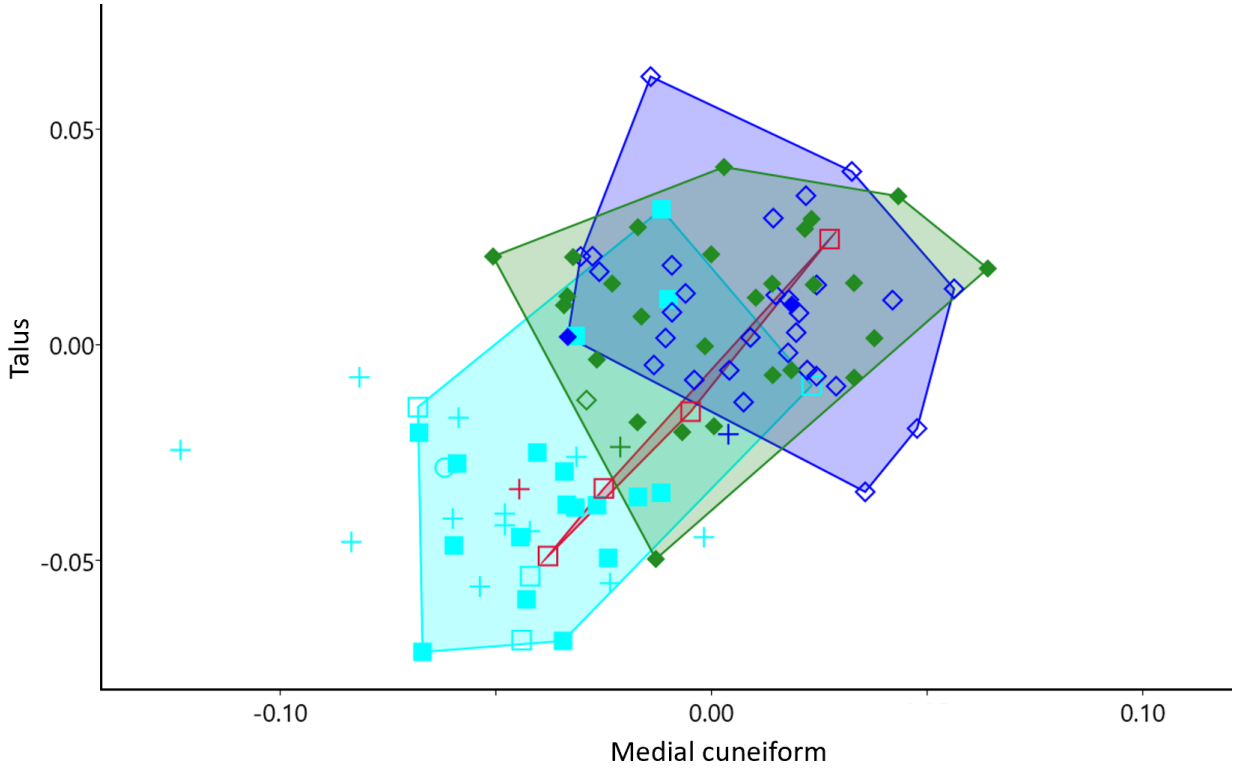

Figure 7. Plot of the PLS analysis generated from the medial cuneiform and talus shape data showing only chimpanzees and captive unknowns accounting for 46% of the total covariance between bones. Captive unknowns are shown as the subspecies to which they were classified by the DFA of the combined talus and medial cuneiform shape data (symbols as in Fig. 4 plus captive unknowns classified as western, light blue crosses; captive unknown classified as Nigeria-Cameroon, red cross; captive unknown classified as central, dark blue cross; captive unknown classified as eastern, green cross). (RETURN TO TEXT)

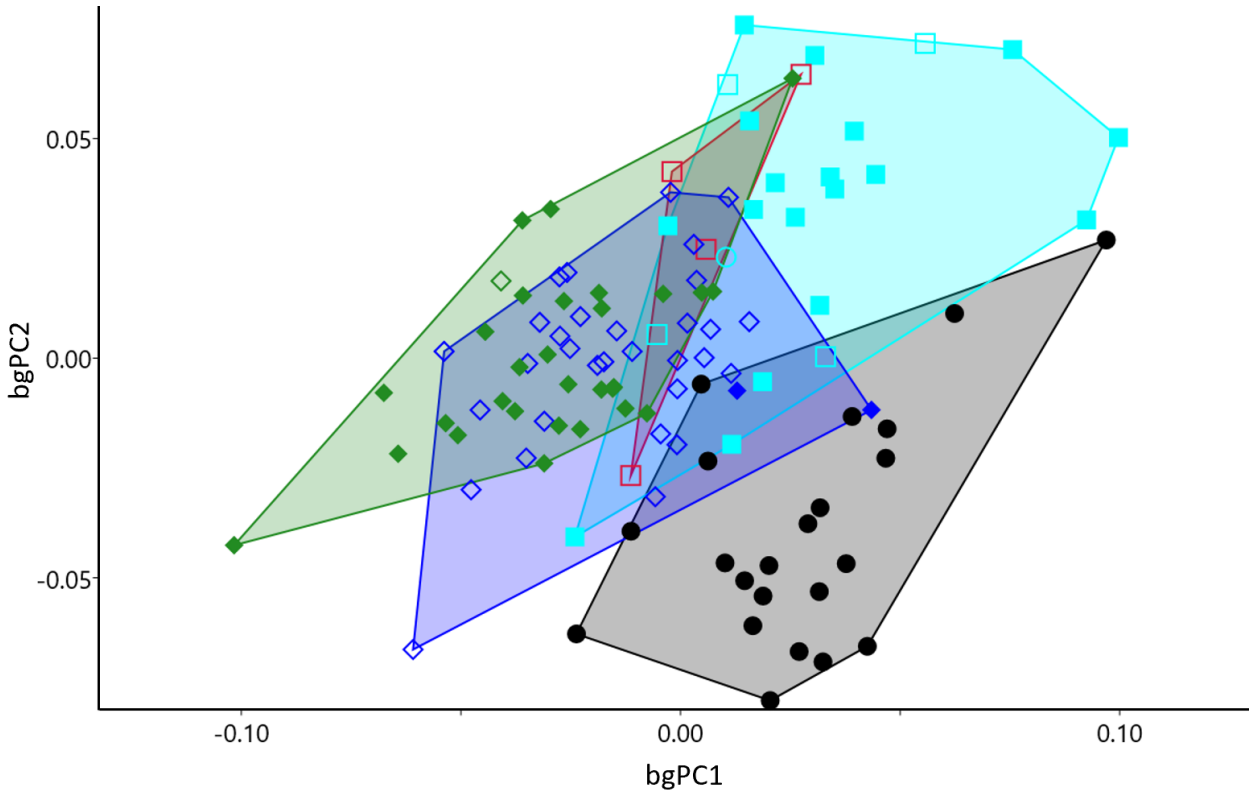

Figure 8. Plot of the between-group principal components (bgPC1 and bgPC2) generated from the talus shape data. bgPC1 accounts for 48.2% of the variation, bgPC2 accounts for 43.8% (symbols as in Fig. 4). (RETURN TO TEXT)

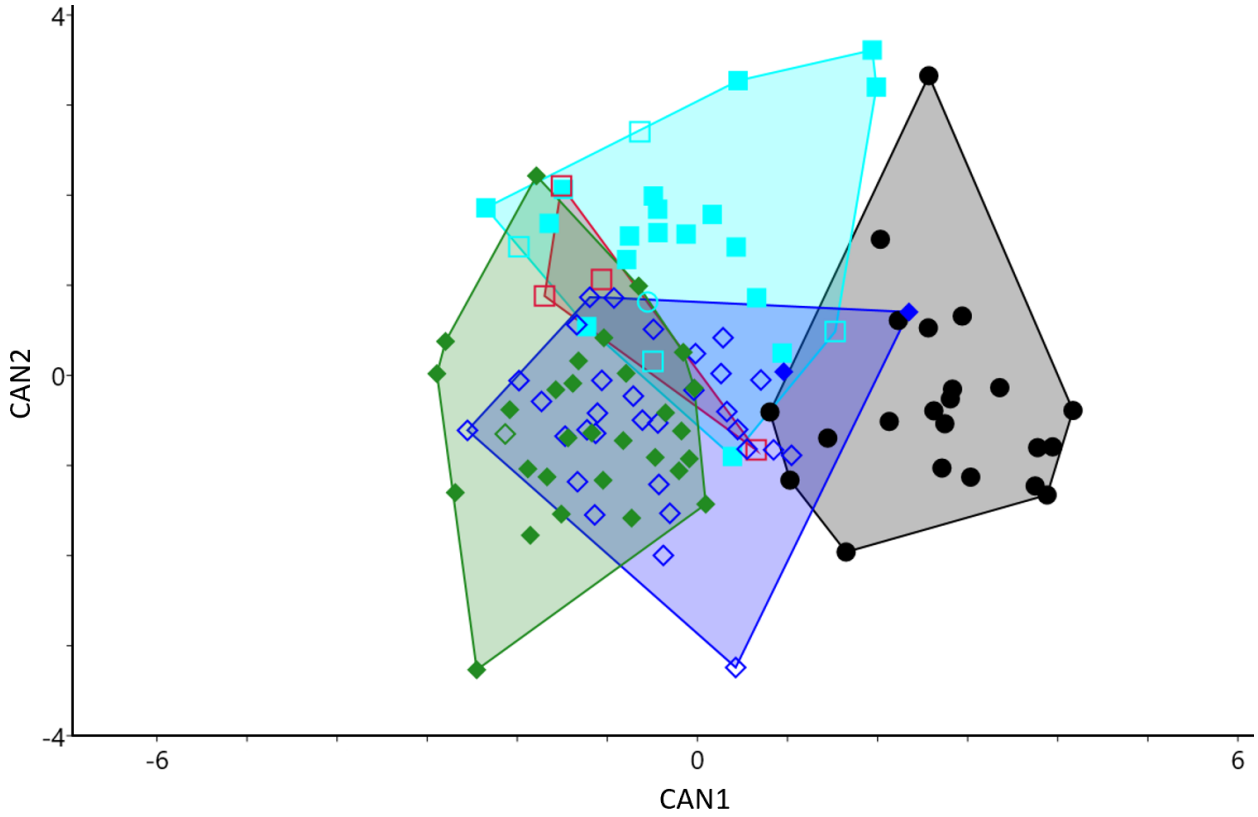

Figure 9. Plot of the canonical variables (CAN1 and CAN2) generated from the talus shape data. CAN1 accounts for 70.5% of the variation, CAN2 accounts for 24.5% (symbols as in Fig. 4). (RETURN TO TEXT)

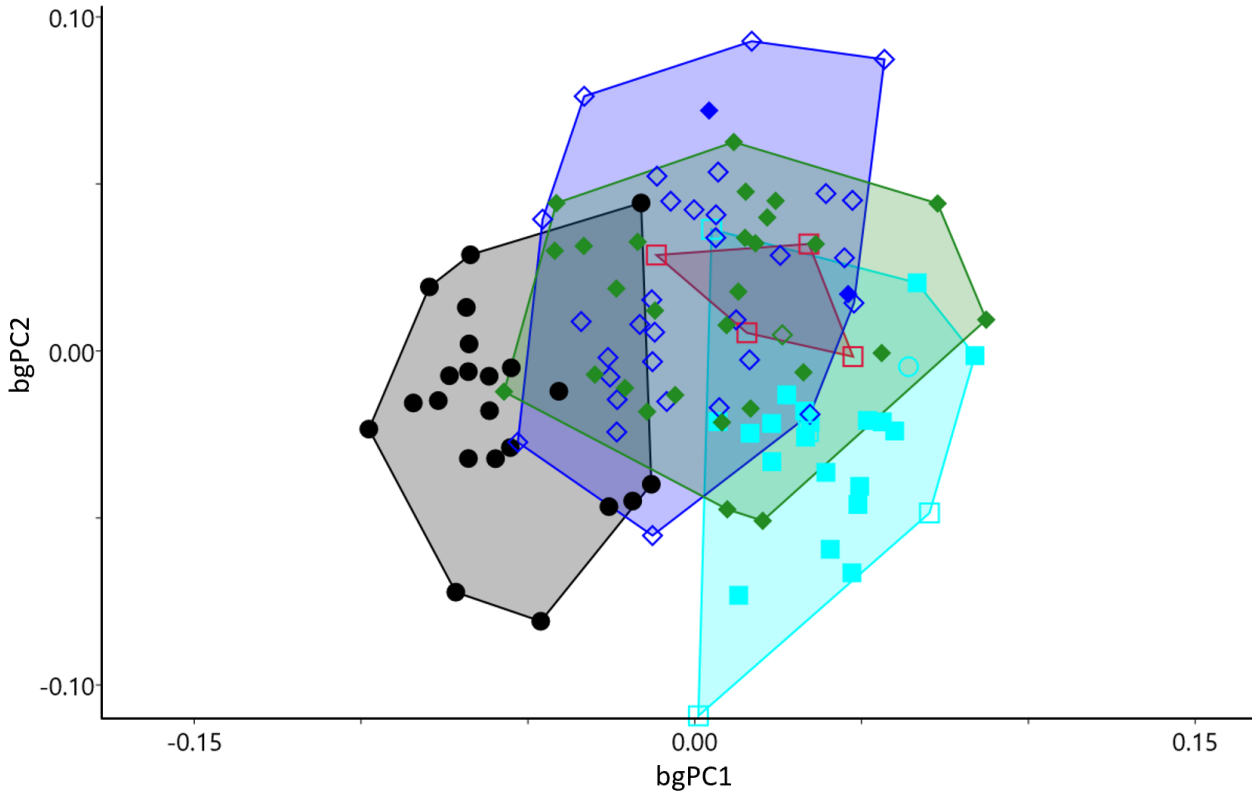

Figure 10. Plot of the between-group principal components (bgPC1 and bgPC2) generated from the medial cuneiform shape data. bgPC1 accounts for 64.8% of the variation, bgPC2 accounts for 26.1% (symbols as in Fig. 4). (RETURN TO TEXT)

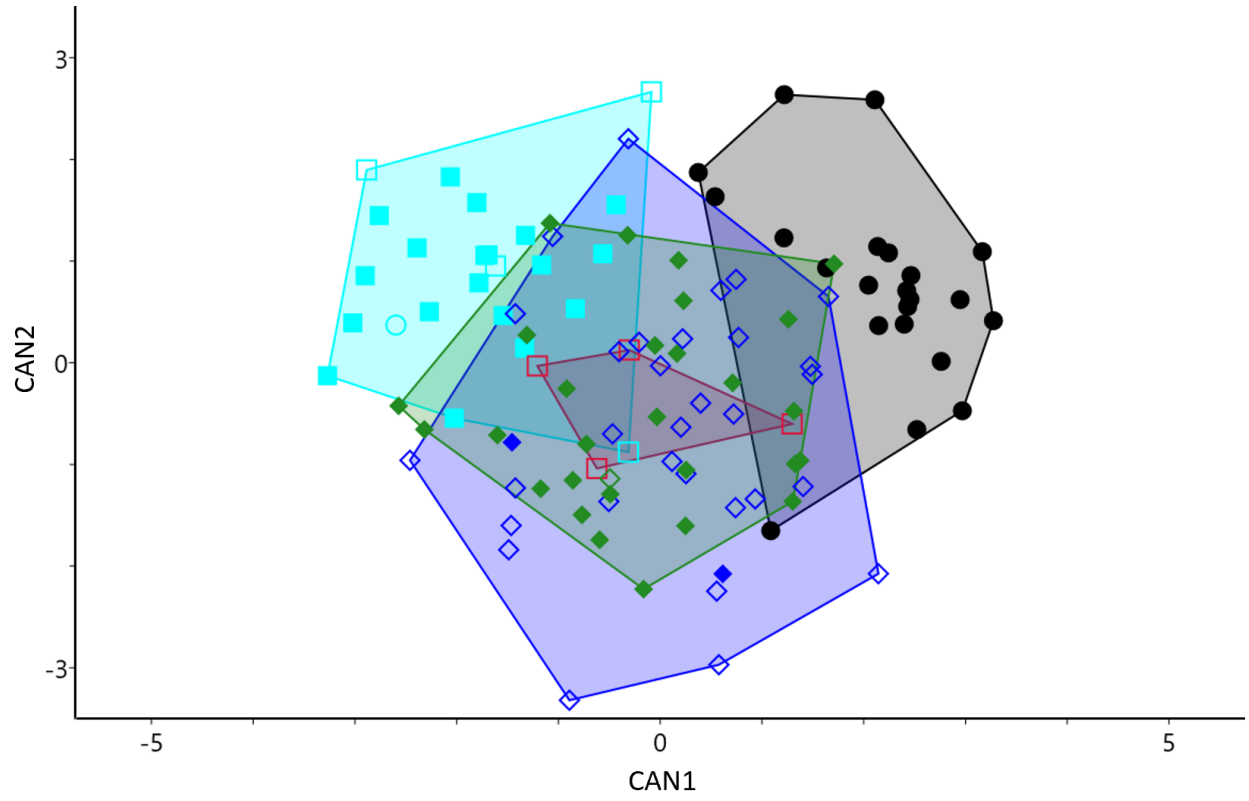

Figure 11. Plot of the canonical variables (CAN1 and CAN2) generated from the medial cuneiform shape data. CAN1 accounts for 72.4% of the variation, CAN2 accounts for 22.0% (symbols as in Fig. 4). (RETURN TO TEXT)

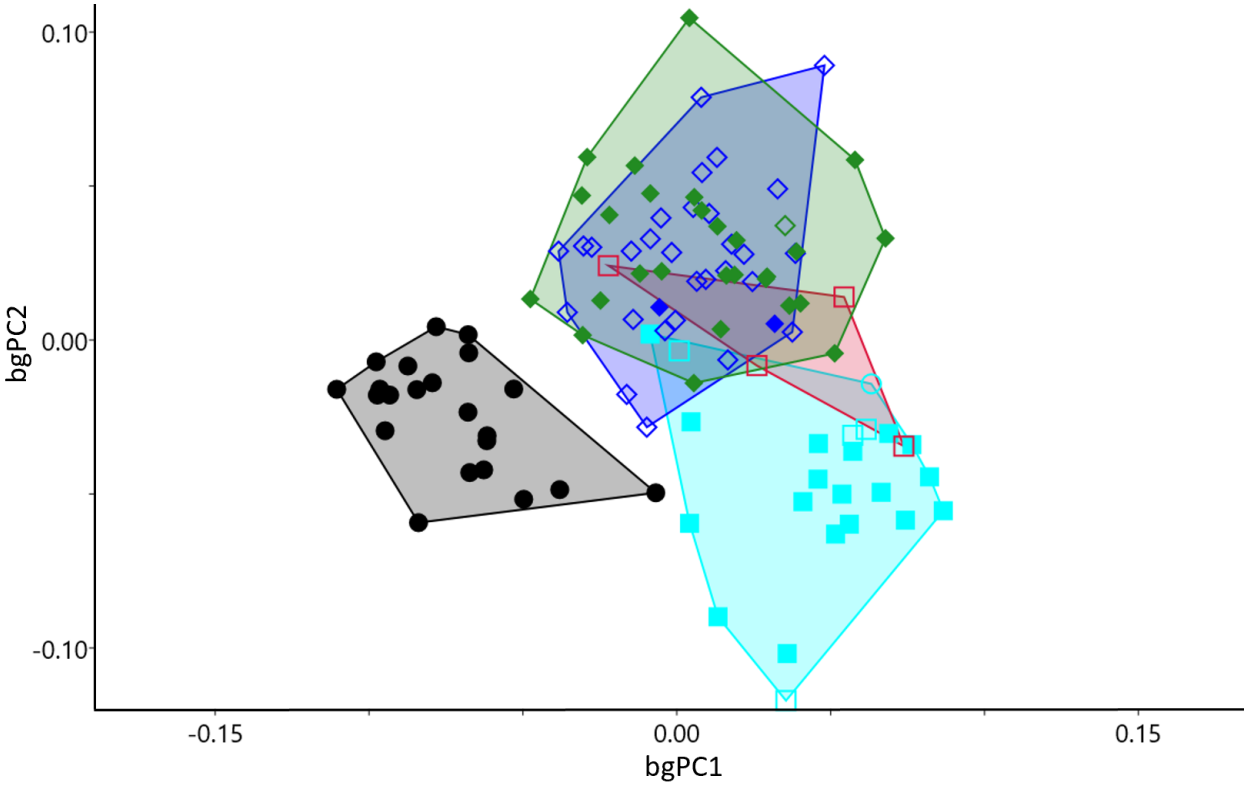

Figure 12. Plot of the between-group principal components (bgPC1 and bgPC2) generated from the combined talus and medial cuneiform shape data. bgPC1 accounts for 55.6% of the variation, bgPC2 accounts for 34.7% (symbols as in Fig. 4). (RETURN TO TEXT)

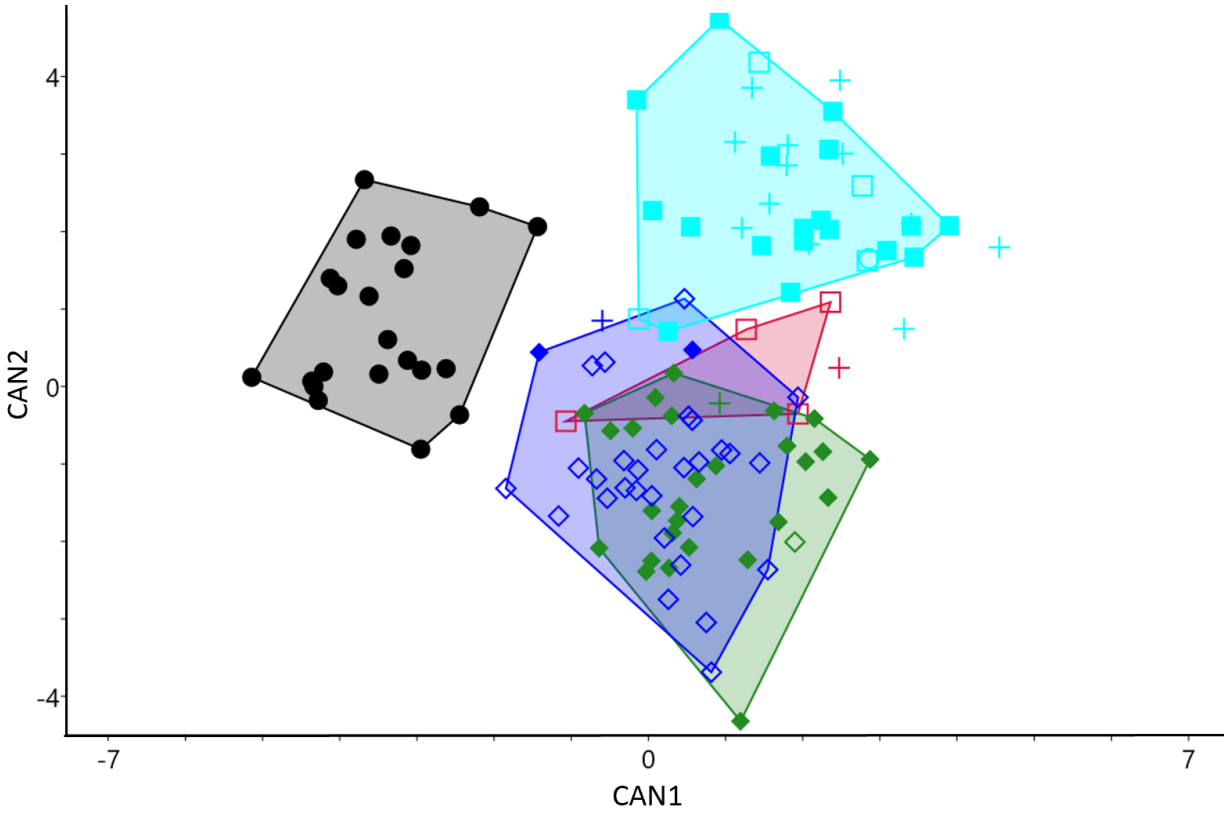

Figure 13. Plot of the canonical variables (CAN1 and CAN2) generated from the combined talus and medial cuneiform shape data. CAN1 accounts for 58.5% of the variation, CAN2 accounts for 36.1% (symbols as in Fig. 7). (RETURN TO TEXT)

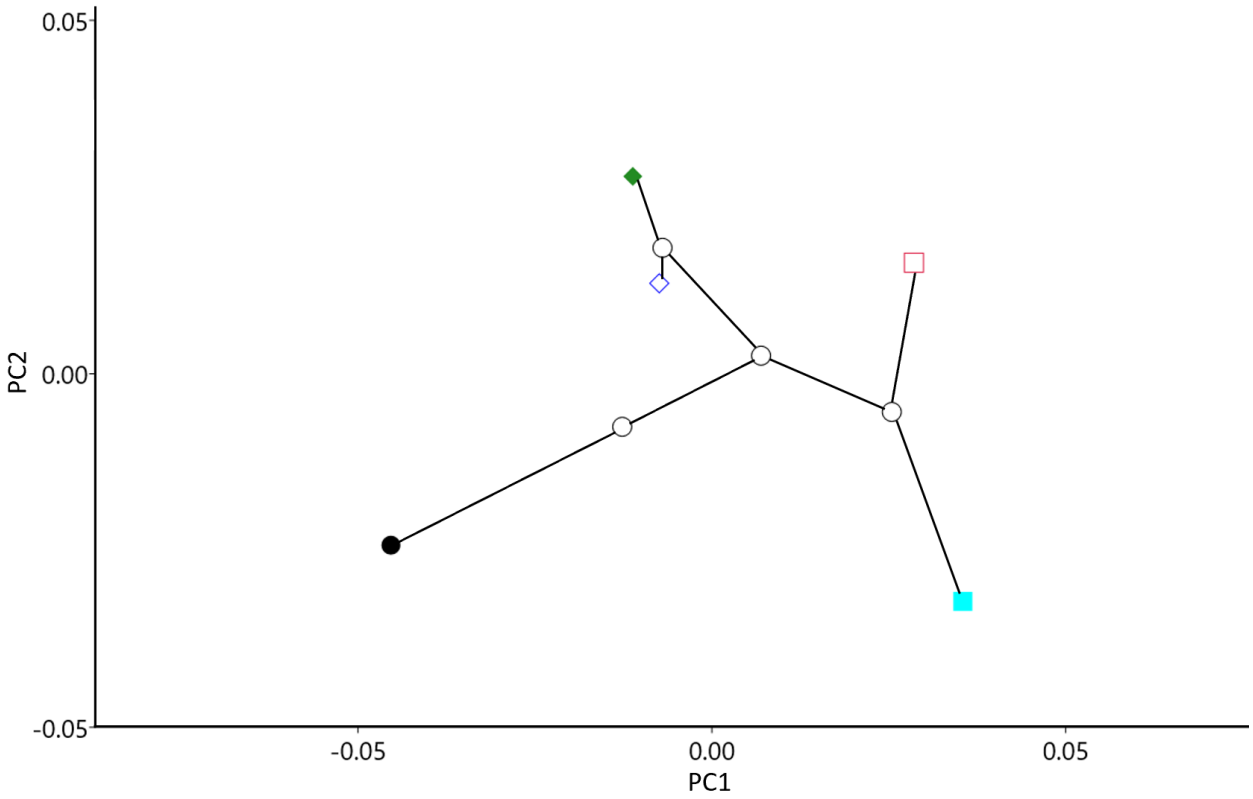

Figure 14. Phylomorphospace analysis of group means from the talus shape data. PC1 represents 42.5% of the variance, PC2 represents 27.8% (bonobos, black solid circle; western chimpanzees, light blue solid square; Nigeria-Cameroon chimpanzees, red open square; central chimpanzees, dark blue open diamond; eastern chimpanzees, green solid diamond; nodes, black open circles). (RETURN TO TEXT)

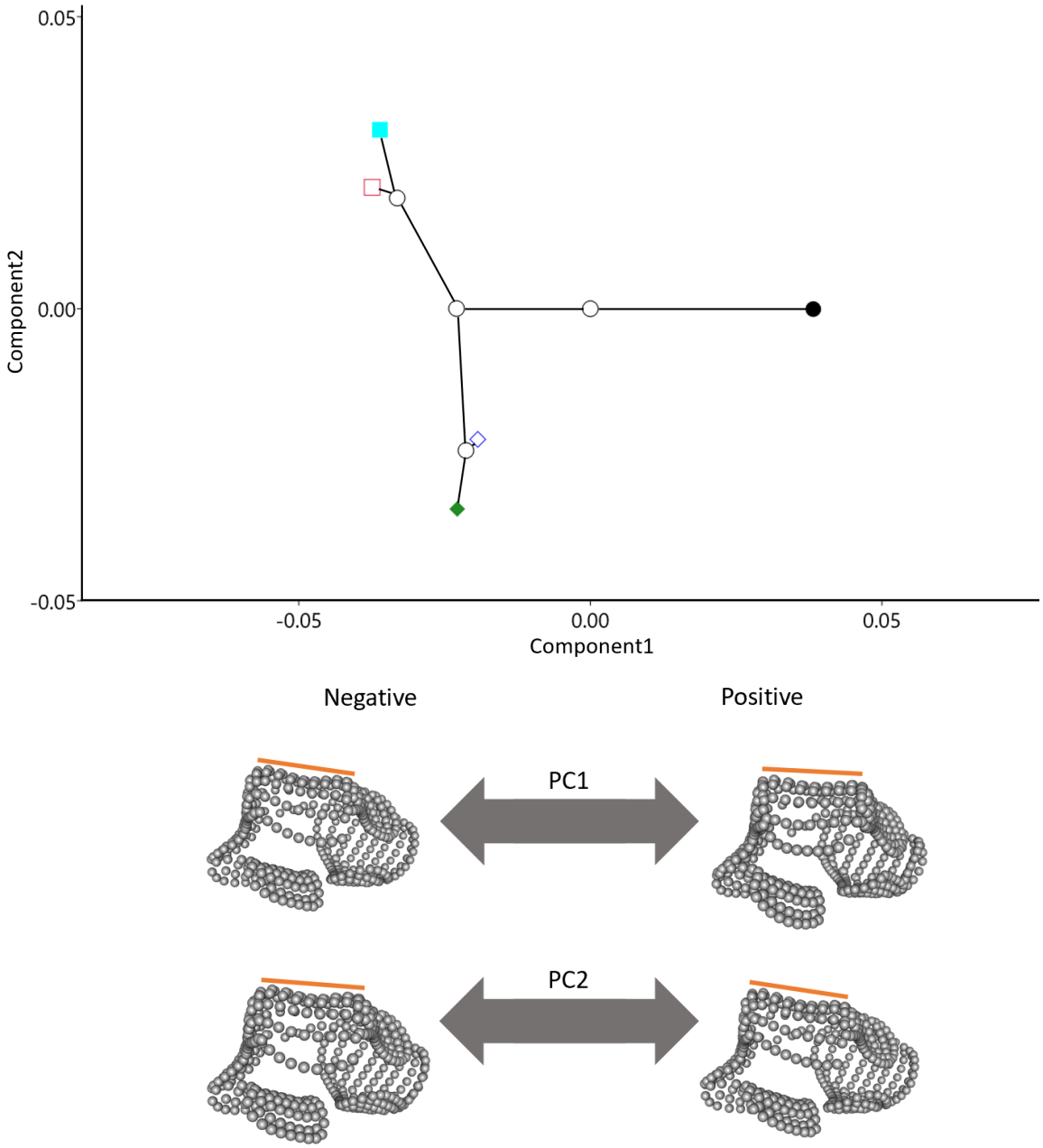

Figure 15. Phylogenetically aligned component analysis of the group means from the talus shape data. Component1 represents 82.6% of the covariance between the medial cuneiform group mean shape data and the phylogenetic covariance matrix based on the phylogenetic relationships between *Pan* taxa, Component2 accounts for 13.9% covariance (symbols as in Fig. 14). (RETURN TO TEXT)

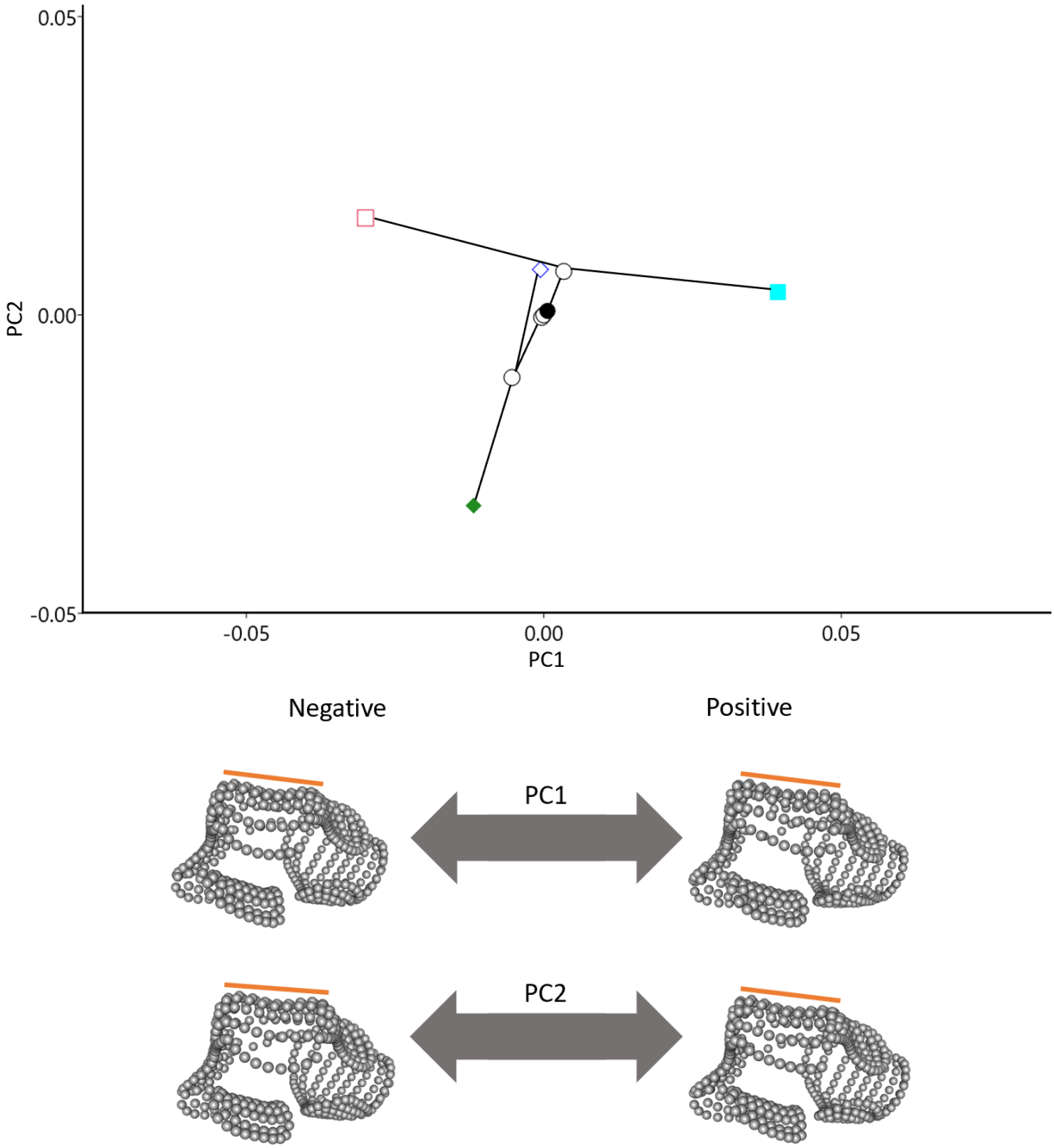

Figure 16. Phylogenetic PCA of the group means from the talus shape data. PC1 represents 49.0% of the variance that is independent of phylogenetic relationships, PC2 represents 29.1% (symbols as in Fig. 14). (RETURN TO TEXT)

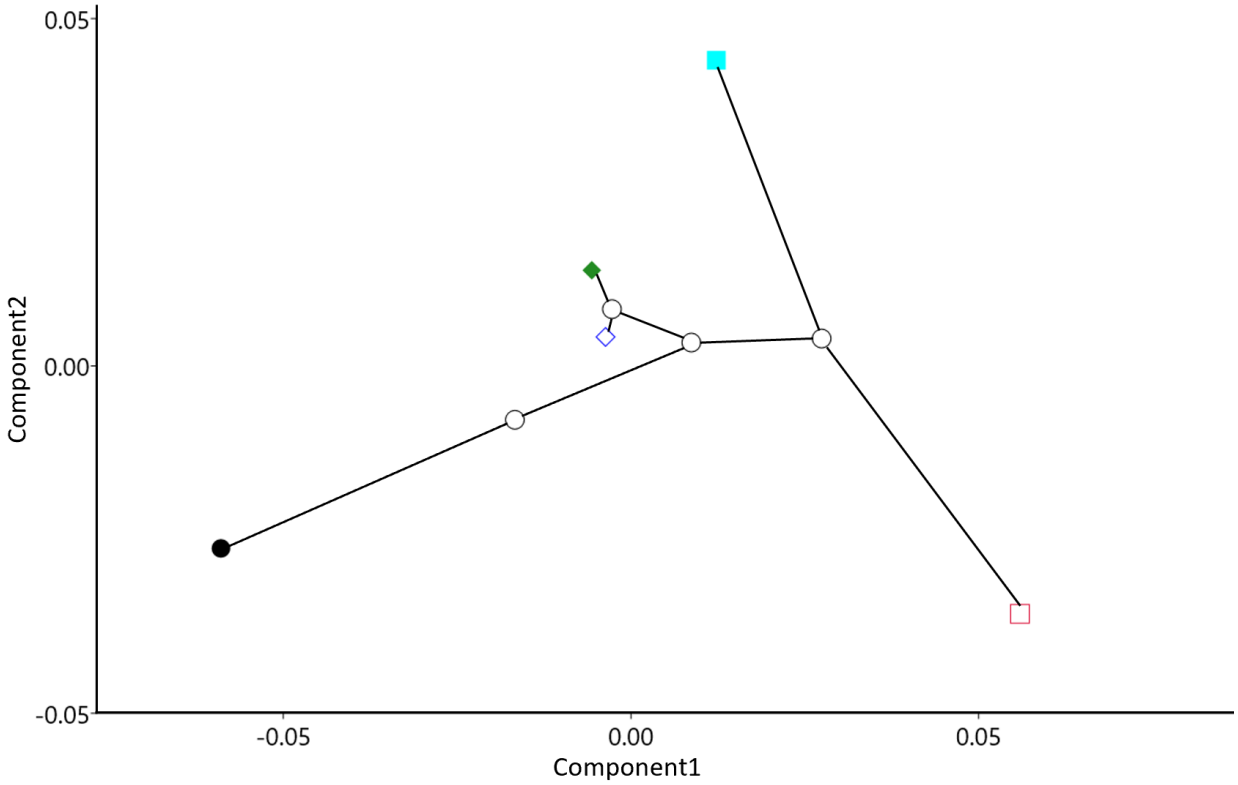

Figure 17. Phylomorphospace analysis of group means from the medial cuneiform shape data. PC1 represents 51.3% of the variance, PC2 represents 30.9% (symbols as in Fig. 14). (RETURN TO TEXT)

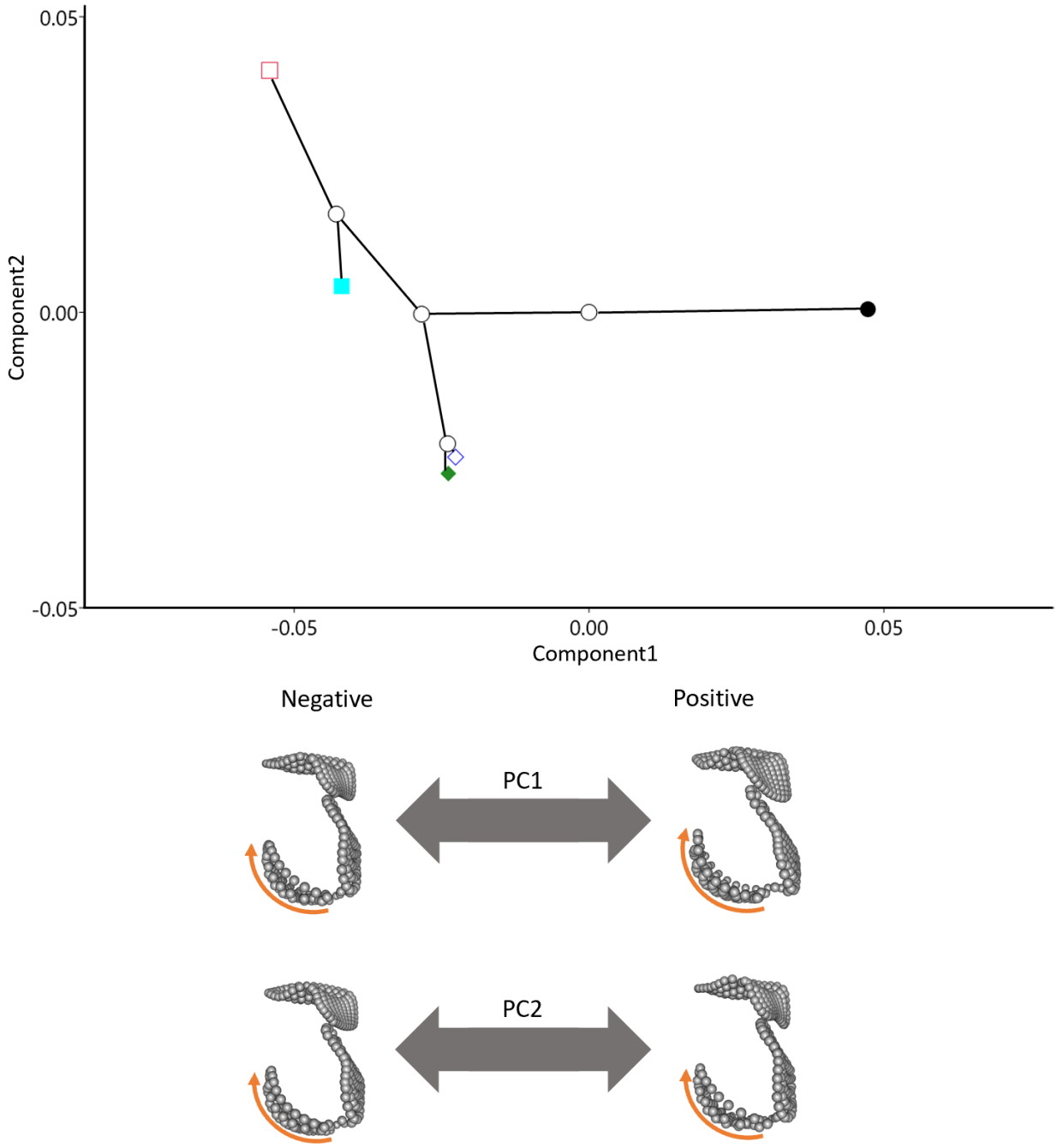

Figure 18. Phylogenetically aligned component analysis of the group means from the medial cuneiform shape data. Component1 represents 88.3% of the covariance between the medial cuneiform group mean shape data and the phylogenetic covariance matrix based on the phylogenetic relationships between *Pan* taxa, Component2 accounts for 8.41% covariance (symbols as in Fig. 14). (RETURN TO TEXT)

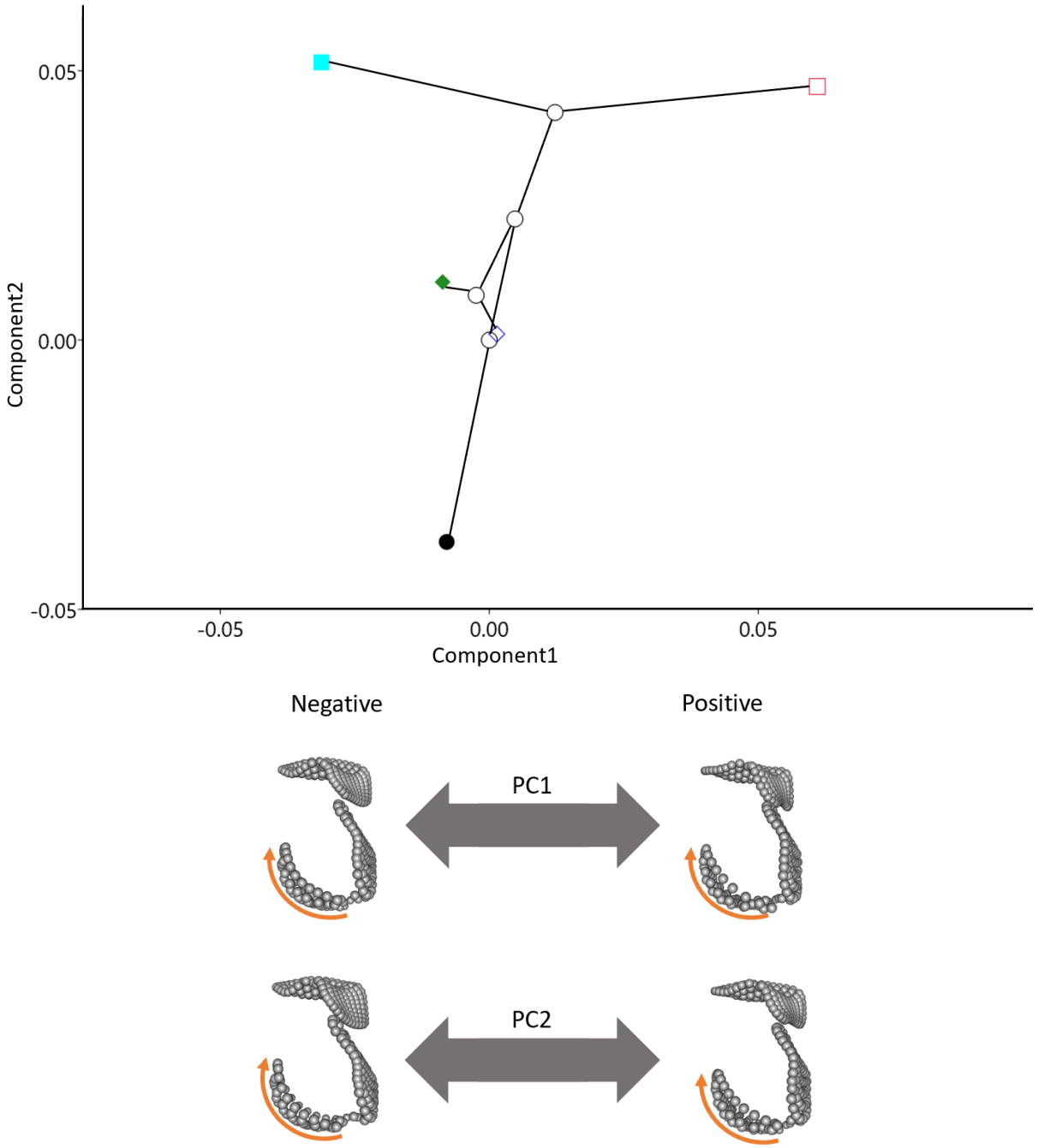

Figure 19. Phylogenetic PCA of the group means from the medial cuneiform shape data. PC1 represents 68.9% of the variance that is independent of phylogenetic relationships, PC2 represents 15.1% (symbols as in Fig. 14). (RETURN TO TEXT)

Tables

Table 1: Frequency of arboreal locomotor behaviours from quantitative studies of bonobo locomotor behaviour. Values are given in percentages* of locomotor bouts from the publications of these quantitative studies. (RETURN TO TEXT)

Study site		Lomako		LuiKotale
Source	Susman et al., 1980	Susman, 1984	Doran, 1993a	Ramos, 2014
Habituated?	No	No	No	Yes
	Bouts (%)	Bouts (%)	Bouts (%)	Bouts (%)
Quadrupedalism	33	31	35.2	17.6
Climbing & scrambling	20	31	49.4	72.7
Suspension	20	21	10.3	1.8
Bipedality	8	10	1.3	5.8
Leaping & Diving	20	6	3.8	0.0

*Each column may not add to 100 as many percentages obtained from the literature were only given as rounded.

Table 2: Percentage of time spent by chimpanzees and bonobos on the ground and in the trees during the day. (RETURN TO TEXT)

Taxon	Study Site	Sex	Time spent on the ground (%)	Time spent in the trees (%)
*Bonobo	LuiKotale	Male	58.7	41.3
		Female	52.7	47.3
**Western	Tai Forest	Male	51.1	48.9
		Female	35.1	64.8
**Eastern	Mahale	Male	67.1	32.9
		Female	52.2	47.8
**Eastern	Gombe	Male	62.6	37.4
		Female	31.6	68.4

*Values from Ramos (2014)

** Values from Doran and Hunt (1994)

Table 3: Comparison of combined sex averages for arboreal locomotor behaviours from quantitative studies of eastern and western chimpanzees as well as bonobos. Values are given in percentages of locomotor bouts. (RETURN TO TEXT)

Taxon	Eastern	Western		Bonobo	
Study site	Gombe and Mahale	Tai Forest		LuiKotale	
Source	Doran and Hunt, 1994	Doran and Hunt, 1994		Ramos, 2014	
Habituated?	Yes	Yes		Yes	
	Bouts (%)	Bouts (%)		Bouts (%)	
	Male and female*	Male	Female	Male	Female
Quadrupedalism	29.4	11.7	30.3	16.0	20.9
Climbing & scrambling	59.9	76.7	58.8	74.9	70.8
Suspension	8.1	5.8	7.4	2.9	1.1
Bipedality	2.0	5.8	0.8	6.3	5.4
Leaping & Diving	1.2	-	1.6	-	-

*There are no significant differences between the arboreal locomotor frequencies between Gombe and Mahale males and females.

Table 4: Percentage of climbing bouts on small (<10 cm) and large (>10–15 cm) diameter substrates. (RETURN TO TEXT)

Taxon	Source	<10 cm diameter	>10 cm diameter*
Eastern	Hunt, 1992	85%	15%
Western	Doran, 1993b	46.1%	46.8%*
Bonobo	Ramos, 2014	94%	6%

*This is >15 cm for western chimpanzees.

Table 5: Talus and medial cuneiform sample breakdown. (RETURN TO TEXT)

Sample	Taxon	Unknown sex	Female	Male	Wild	Captive	Adults	Sub-adults	Total
Talus	Bonobo	2	10	10	22	0	22	0	22
	Western	7	7	9	18	5	23	0	23
	Nigeria-Cameroon	0	3	1	4	0	4	0	4
	Central	4	13	16	31	2	32	1	33
	Eastern	11	7	12	29	1	24	6	30
	Unknown	3	8	4	0	15	15	0	15
	Total								**127**
Medial cuneiform	Bonobo	2	10	10	22	0	22	0	22
	Western	7	8	9	19	5	24	0	24
	Nigeria-Cameroon	0	3	1	4	0	4	0	4
	Central	3	13	17	31	2	32	1	33
	Eastern	12	7	10	28	1	23	6	29
	Unknown	3	8	4	0	15	15	0	15
	Total								**127**
Paired	Bonobo	2	10	10	22	0	22	0	22
	Western	7	7	9	18	5	23	0	23
	Nigeria-Cameroon	0	3	1	4	0	4	0	4
	Central	3	13	15	31	2	32	1	31
	Eastern	11	7	10	28	1	23	6	28
	Unknown	3	8	4	0	15	15	0	15
	Total								**123**

Table 6: Medial cuneiform landmarks (modified from Harcourt-Smith, 2002) where corner anchor points were placed. (RETURN TO TEXT)

Number	Description
1	Most dorsal point on the navicular facet
2	Most proximo-medial point on the navicular facet
3	Most proximo-plantar point on the navicular facet
4	Most lateral point on the navicular facet
5	Most dorso-lateral point on the first metatarsal facet
6	Most plantar-lateral point on the first metatarsal facet
7	Most plantar-medial point on the first metatarsal facet
8	Most dorso-medial point on the first metatarsal facet
9	Most disto-lateral point on the second metatarsal facet
10	Most disto-medial point on the second metatarsal facet
11	Most proximo-medial point on the distal portion of the intermediate cuneiform facet
12	Most proximo-lateral point on the distal portion of the intermediate cuneiform facet
13	Most dorsal point of contact between the proximal portion of the intermediate cuneiform facet and the navicular facet
14	Most plantar point of contact between the proximal portion of the intermediate cuneiform facet and the navicular facet
15	Most disto-plantar point of proximal portion of the intermediate cuneiform facet
16	Most disto-dorsal point of proximal portion of the intermediate cuneiform facet

Table 7: Talus landmarks (modified from Harcourt-Smith, 2002) where corner anchor points were placed. (RETURN TO TEXT)

Number	Description
1	Most disto-lateral point on the proximal calcaneal facet
2	Most proximo-lateral point on the proximal calcaneal facet
3	Most proximo-medial point on the proximal calcaneal facet
4	Most disto-medial point on the proximal calcaneal facet
5	Most lateral point of contact between the distal calcaneal facet and the navicular facet
6	Most medial point on the lateral edge of the distal calcaneal facet
7	Most proximo-medial point on the distal calcaneal facet
8	Most medial point of contact between the distal calcaneal facet and the navicular facet
9	Most medial point on the navicular facet
10	Most dorsal point on the navicular facet
11	Most distal point of contact between the trochlea and the medial malleolar facet
12	Most proximal point of the medial trochlear rim
13	Most proximal point of the lateral trochlear rim
14	Most distal point of the lateral trochlear rim
15	Most proximal point of contact between the trochlea and the medial malleolar facet
16	Most plantar point on the medial malleolar facet
17	Most dorsal point on the plantar margin of the medial malleolar facet
18	Most proximal point of contact between the trochlea and the lateral malleolar facet
19	Most distal point on the proximal margin of the lateral malleolar facet
20	Most plantar point on the lateral malleolar facet
21	Most distal point on the lateral malleolar facet

Table 8. Percent variance and percent cumulative variance explained of each principal component representing 1% or more of the total variance. (RETURN TO TEXT)

	Medial cuneiform		Talus	
Principal component	% Variance	% Cumulative variance	% Variance	% Cumulative variance
1	14.5	14.5	13.8	13.8
2	13.0	27.5	8.3	22.1
3	9.5	37.0	7.4	29.5
4	7.3	44.3	6.6	36.1
5	6.5	50.8	5.4	41.5
6	4.2	55	4.7	46.2
7	3.7	58.7	4.5	50.7
8	3.4	62.1	3.5	54.2
9	3.2	65.3	3.2	57.4
10	2.7	68.0	3.0	60.4
11	2.5	70.5	2.5	62.9
12	2.2	72.7	2.3	65.2
13	2.2	74.9	2.2	67.4
14	2.0	76.9	1.9	69.3
15	1.6	78.5	1.8	71.1
16	1.6	80.1	1.6	72.7
17	1.4	81.5	1.5	74.2
18	1.3	82.8	1.4	75.6
19	1.2	84.0	1.3	76.9
20	1.1	85.1	1.2	78.1
21	1.0	86.1	1.1	79.2
22	-	-	1.1	80.3

Table 9. Results of post-hoc pairwise tests of the Procrustes distances between pairs of group mean talus shapes. Asterisks indicate statistical significance ($p < .005$) using a Bonferroni correction for multiple comparisons. Chimpanzees of unknown subspecies were omitted from the PERMANOVA and pairwise tests. (RETURN TO TEXT)

	Procrustes distance	p-value
Bonobo: Nigeria-Cameroon	0.08524588	0.008
Bonobo: Eastern	0.07198114	0.001*
Bonobo: Central	0.06437852	0.001*
Bonobo: Western	0.07843221	0.001*
Nigeria-Cameroon: Eastern	0.06890361	0.089
Nigeria-Cameroon: Central	0.06291812	0.200
Nigeria-Cameroon: Western	0.05998692	0.377
Eastern: Central	0.04154869	0.003*
Eastern: Western	0.07378634	0.001*
Central: Western	0.06318049	0.001*

Table 10. Results of post-hoc pairwise test of the Procrustes distance between pairs of group mean medial cuneiform shapes. Asterisks indicate statistical significance ($p < .005$) using a Bonferroni correction for multiple comparisons. Chimpanzees of unknown subspecies were omitted from the PERMANOVA and pairwise tests. (RETURN TO TEXT)

	Procrustes distance	p-value
Bonobo: Nigeria-Cameroon	0.11560512	0.002*
Bonobo: Eastern	0.07769158	0.001*
Bonobo: Central	0.07605941	0.001*
Bonobo: Western	0.10047978	0.001*
Nigeria-Cameroon: Eastern	0.08514197	0.025
Nigeria-Cameroon: Central	0.07985044	0.045
Nigeria-Cameroon: Western	0.09250468	0.016
Eastern: Central	0.03005799	0.365
Eastern: Western	0.06014632	0.001*
Central: Western	0.06598794	0.001*

References

Abwe, E.E., Morgan, B.J., Tchiengue, B., Kentatchime, F., Doudja, R., Ketchen, M.E., Teguia, E., Ambahe, R., Venditti, D.M., Mitchell, M.W., Fosso, B., Mounga, A., Fotso, R.C., Gonder, M.K., 2019. Habitat differentiation among three Nigeria–Cameroon chimpanzee (*Pan troglodytes ellioti*) populations. Ecology and Evolution. 9, 1489–1500.

Adams, D., 2014. A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. Systematic biology 63, 685–697.

Adams, D., Otarola-Castillo, E., 2013. Geomorph: An R package for the collection and analysis of geometric morphometric shape data. Methods in Ecology and Evolution 4, 393–399.

Aiello, L., Dean, C., 2002. An Introduction to Human Evolutionary Anatomy. Elsevier Academic Press, London.

Anderson, M., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.

Badrian, A.J., Badrian, N.L., 1977. Pygmy chimpanzees. Oryx 14, 463–472.

Badrian, N., Badrian, A., Susman, R.L.S., 1981. Preliminary observations on the feeding behavior of *Pan paniscus* in the Lomako forest of central Zaire. Primates 22, 173–181.

Bardua, C., Wilkinson, M., Gower, D.J., Sherratt, E., Goswami, A., 2019. Morphological evolution and modularity of the caecilian skull. BMC Evolutionary Biology 19, 30.

Bello‐Hellegouarch, G., Potau, J.M., Arias‐Martorell, J., Pastor, J.F., Pérez‐Pérez, A., 2013. Morphological effects of captivity: A geometric morphometric analysis of the dorsal side of the scapula in captive-bred and wild-caught hominoidea. American Journal of Physical Anthropology 152, 306–310.

Berillon, G., 1999. Geometric pattern of the hominoid hallucal tarsometatarsal complex: Quantifying the degree of hallux abduction in early hominids. Comptes Rendus de l'Académie des Sciences Series IIA 328, 627–633.

Blomberg, S.P., Garland, T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution; International Journal of Organic Evolution 57, 717–745.

Boesch, C., 1978. Nouvelles observations sur les chimpanzes de la foret de Tai (Cote D'Ivoire). La Terre et la Vie 32, 195–201.

Boesch, C., Boesch-Achermann, H., 2000. The chimpanzees of the Taï Forest: Behavioural ecology and evolution. Oxford University Press, Oxford, United Kingdom. pp. 1–14.

Boesch, C., Head, J., Robbins, M.M., 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. Journal of Human Evolution 56, 560–569.

Boesch, C., Wittig, R., Crockford, C., Vigilant, L., Deschner, T., Leendertz, F. (Eds), 2019. The chimpanzees of the Taï Forest: 40 years of research. Cambridge University Press, Cambridge, United Kingdom.

Bogart, S.L., Pruetz, J.D., 2011. Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. American Journal of Physical Anthropology. 145, 11–20.

Bookstein, F.L., 2017. A newly noticed formula enforces fundamental limits on geometric morphometric analyses. Evolutionary Biology 44, 522–541.

Bookstein, F.L., 2019. Pathologies of between-groups principal components analysis in geometric morphometrics. Evolutionary Biology 46, 271–302.

Boulesteix, A.-L., 2005. A note on between-group PCA. International Journal of Pure Applied Math 19, 359–366.

Brand, C.M., White, F.J., Wakefield, M.L., Waller, M.T., Ruiz-López, M.J., Ting, N., 2016. Initiation of genetic demographic monitoring of bonobos (*Pan paniscus*) at Iyema, Lomako Forest, DRC. Primate Conservation 30, 103–111.

Cardini, A., 2019. Integration and modularity in procrustes shape data: Is there a risk of spurious results? Evolutionary Biology 46, 90–105.

Cardini, A., 2020a. Modern morphometrics and the study of population differences: Good data behind clever analyses and cool pictures? The Anatomical Record 303, 2747–2765.

Cardini, A., 2020b. Less tautology, more biology? A comment on "high-density" morphometrics. Zoomorphology 139, 513–529.

Cardini, A., O'Higgins, P., Rohlf, F.J., 2019. Seeing distinct groups where there are none: Spurious patterns from between-group PCA. Evolutionary Biology 46, 303–316.

Cardini, A., Polly, P.D., 2020. Cross-validated between group PCA catterplots: A solution to spurious group separation? Evolutionary Biology 47, 85–95.

Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., Ranzuglia, G., 2008. MeshLab: An open-source mesh processing tool. Sixth Eurographics Italian Chapter Conference, 129–136.

Clarke, R.J., Tobias, P.V., 1995. Sterkfontein member 2 foot bones of the oldest South African hominid. Science 269, 521–524.

Collyer, M.L., Adams, D.C., 2020. Phylogenetically aligned component analysis. Methods in Ecology and Evolution 12. 359–372.

Collyer, M.L., Adams, D.C., 2021. RRPP: Linear Model Evaluation with Randomized Residuals in a Permutation Procedure, R package version 0.6.2. https://cran.r-project.org/package=RRPP.

Collyer, M.L., Adams, D.C., 2018. RRPP: An R package for fitting linear models to high‐dimensional data using residual randomization. https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210X.13029.

de Manuel, M. de, Kuhlwilm, M., Frandsen, P., Sousa, V.C., Desai, T., Prado-Martinez, J., Hernandez-Rodriguez, J., Dupanloup, I., Lao, O., Hallast, P., Schmidt, J.M., Heredia-Genestar, J.M., Benazzo, A., Barbujani, G., Peter, B.M., Kuderna, L.F.K., Casals, F., Angedakin, S., Arandjelovic, M., Boesch, C., Kühl, H., Vigilant, L., Langergraber, K., Novembre, J., Gut, M., Gut, I., Navarro, A., Carlsen, F., Andrés, A.M., Siegismund, H.R., Scally, A., Excoffier, L., Tyler-Smith, C., Castellano, S., Xue, Y., Hvilsom, C., Marques-Bonet, T., 2016. Chimpanzee genomic diversity reveals ancient admixture with bonobos. Science 354, 477–481.

DeSilva, J.M., 2009. Functional morphology of the ankle and the likelihood of climbing in early hominins. Proceedings of the National Academy of Sciences 106, 6567–6572.

DeSilva, J., McNutt, E., Benoit, J., Zipfel, B., 2018. One small step: A review of Plio-Pleistocene hominin foot evolution. American Journal of Physical Anthropology 168, 63–140.

Doran, D.M., 1992. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: A case study of paedomorphism and its behavioral correlates. Journal of Human Evolution 23, 139–157.

Doran, D.M., 1993a. Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. American Journal of Physical Anthropology 91, 83–98.

Doran, D.M., 1993b. Sex differences in adult chimpanzee positional behavior: The influence of body size on locomotion and posture. American Journal of Physical Anthropology 91, 99–115.
Doran, D.M., 1996. Comparative positional behaviour of the African apes. In: McGrew, W., Marchant, L., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, United Kingdom. pp. 213–224.
Doran, D.M., 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. Journal of Human Evolution 32, 323–344.
Doran, D.M., Hunt, K.D., 1994. Comparative locomotion behaviour of chimpanzees and bonobos: Species and habitat differences. In: Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., Heltne, P.G. (Eds), Chimpanzee Cultures. Harvard University Press, Cambridge, Massachusetts. pp. 93–108.
Druelle, F., Aerts, P., Ngawolo, J.C.B., Narat, V., 2020. Impressive arboreal gap-crossing behaviors in wild bonobos, *Pan paniscus*. International Journal of Primatology. 41, 129–140.
Dunn, R.H., Tocheri, M.W., Orr, C.M., Jungers, W.L., 2014. Ecological divergence and talar morphology in gorillas. American Journal of Physical Anthropology 153, 526–541.
Ely, J.J., Dye, B., Frels, W.I., Fritz, J., Gagneux, P., Khun, H.H., Switzer, W.M., Lee, D.R., 2005. Subspecies composition and founder contribution of the captive U.S. chimpanzee (*Pan troglodytes*) population. American Journal of Primatology. 67, 223–241.
Fischer, A., Prüfer, K., Good, J.M., Halbwax, M., Wiebe, V., André, C., Atencia, R., Mugisha, L., Ptak, S.E., Pääbo, S., 2011. Bonobos fall within the genomic variation of chimpanzees. PLoS ONE 6, e21605.
Gonder, M.K., Disotell, T.R., Oates, J.F., 2006. New genetic evidence on the evolution of chimpanzee populations and implications for taxonomy. International Journal of Primatology 27, 1103–1127.
Gonder, M.K., Locatelli, S., Ghobrial, L., Mitchell, M.W., Kujawski, J.T., Lankester, F.J., Stewart, C.-B., Tishkoff, S.A., 2011. Evidence from Cameroon reveals differences in the genetic structure and histories of chimpanzee populations. Proceedings of the National Academy of Sciences 108, 4766–4771.
Goodall, J., 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Animal Behaviour Monographs 1, 161–311.
Goodall, J., 1986. The chimpanzees of Gombe: Patterns of behavior. Harvard University Press, Cambridge, Massachusetts.
Goodman, M., 1999. The genomic record of Humankind's evolutionary roots. American Journal of Human Genetics 64, 31–39.
Goswami, A., Watanabe, A., Felice, R.N., Bardua, C., Fabre, A.-C., Polly, P.D., 2019. High-density morphometric analysis of shape and integration: The good, the bad, and the not-really-a-problem. Integrative and Comparative Biology 59, 669–683.
Gower, J.C., 1975. Generalized Procrustes analysis. Psychometrika 40, 33–51.
Harcourt-Smith, W.E.H., 2016. Early hominin diversity and the emergence of the genus *Homo*. Journal of Anthropological Science 94, 19–27.
Harcourt-Smith, W.E.H., 2002. Form and function in the hominoid tarsal skeletal structure. PhD dissertation, University College London, London.

Harcourt-Smith, W.E.H., Aiello, L.C., 2004. Fossils, feet and the evolution of human bipedal locomotion. Journal of Anatomy 204, 403–416.
Harcourt-Smith, W.E.H., Throckmorton, Z., Congdon, K.A., Zipfel, B., Deane, A.S., Drapeau, M.S.M., Churchill, S.E., Berger, L.R., DeSilva, J.M., 2015. The foot of *Homo naledi*. Nature Communications 6, 8432.
Hohmann, G., Fruth, B., 2003. Lui Kotal - A new site for field research on bonobos in the Salonga National Park. Pan Africa News 10, 25–27.
Hohmann, G., Ortmann, S., Remer, T., Fruth, B., 2019. Fishing for iodine: What aquatic foraging by bonobos tells us about human evolution. BMC Zoology 4, 5.
Holowka, N.B., O'Neill, M.C., Thompson, N.E., Demes, B., 2017a. Chimpanzee ankle and foot joint kinematics: Arboreal versus terrestrial locomotion. American Journal of Physical Anthropology 164, 131–147.
Holowka, N.B., O'Neill, M.C., Thompson, N.E., Demes, B., 2017b. Chimpanzee and human midfoot motion during bipedal walking and the evolution of the longitudinal arch of the foot. Journal of Human Evolution 104, 23–31.
Hunt, K.D, 1989. Positional behavior in *Pan troglodytes* at the Mahale Mountains and the Gombe Stream National Parks, Tanzania. PhD Dissertation. University of Michigan, Ann Arbor, Michigan.
Hunt, K.D., 1991. Positional behavior in the Hominoidea. International Journal of Primatology 12, 95–118.
Hunt, K.D., 1992. Positional behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. American Journal of Physical Anthropology 87, 83–105.
Hunt, K.D., 1994. Body size effects on vertical climbing among chimpanzees. International Journal of Primatology 15, 855–865.
Hunt, K.D., Cant, J.G.H., Gebo, D.L., Rose, M.D., Walker, S.E., Youlatos, D., 1996. Standardized descriptions of primate locomotor and postural modes. Primates 37, 363–387.
Johnson, R.A., Wichern, D.W., 2002. Applied multivariate statistical analysis. Prentice-Hall Inc, Upper Saddle River, NJ.
Jungers, W.L., Larson, S.G., Harcourt-Smith, W., Morwood, M.J., Sutikna, T., Due Awe, R., Djubiantono, T., 2009. Descriptions of the lower limb skeleton of *Homo floresiensis*. Journal of Human Evolution 57, 538–554.
Jungers, W.L., Stern, J.T., 1983. Body proportions, skeletal allometry and locomotion in the hadar hominids: A reply to Wolpoff. Journal of Human Evolution 12, 673–684.
Kamgang, S.A., Bobo, K.S., Maisels, F., Ambahe, R.D.D., Ambassa Ongono, D.E., Gonder, M.K., Johnson, P., Marino, J., Sinsin, B., 2018. The relationship between the abundance of the Nigeria Cameroon chimpanzee (*Pan troglodytes ellioti*) and its habitat: A conservation concern in Mbam Djerem National Park, Cameroon. BMC Ecology 18, 40.
Kano, T., 1980. Social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. Journal of Human Evolution 9, 243–260.
Kidd, R.S., O'Higgins, P., Oxnard, C.E., 1996. The OH8 foot: A reappraisal of the functional morphology of the hindfoot utilizing a multivariate analysis. Journal of Human Evolution 31, 269–291.
Klingenberg, C., Monteiro, L., 2005. Distances and directions in multidimensional shape spaces: Implications for morphometric applications. Systematic Biology 54, 678–88.

Knigge, R.P., Tocheri, M.W., Orr, C.M., Mcnulty, K.P., 2015. Three-dimensional geometric morphometric analysis of talar morphology in extant gorilla taxa from highland and lowland habitats. Anatomical Record 298, 277–290.

Latimer, B., Ohman, J.C., Lovejoy, C.O., 1987. Talocrural joint in African hominoids: Implications for Australopithecus afarensis. American Journal of Physical Anthropology 74, 155–175.

Lester, J.D., Vigilant, L., Gratton, P., McCarthy, M.S., Barratt, C.D., Dieguez, P., Agbor, A., Álvarez-Varona, P., Angedakin, S., Ayimisin, E.A., Bailey, E., Bessone, M., Brazzola, G., Chancellor, R., Cohen, H., Danquah, E., Deschner, T., Egbe, V.E., Eno-Nku, M., Goedmakers, A., Granjon, A.-C., Head, J., Hedwig, D., Hernandez-Aguilar, R.A., Jeffery, K.J., Jones, S., Junker, J., Kadam, P., Kaiser, M., Kalan, A.K., Kehoe, L., Kienast, I., Langergraber, K.E., Lapuente, J., Laudisoit, A., Lee, K., Marrocoli, S., Mihindou, V., Morgan, D., Muhanguzi, G., Neil, E., Nicholl, S., Orbell, C., Ormsby, L.J., Pacheco, L., Piel, A., Robbins, M.M., Rundus, A., Sanz, C., Sciaky, L., Siaka, A.M., Städele, V., Stewart, F., Tagg, N., Ton, E., van Schijndel, J., Vyalengerera, M.K., Wessling, E.G., Willie, J., Wittig, R.M., Yuh, Y.G., Yurkiw, K., Zuberbuehler, K., Boesch, C., Kühl, H.S., Arandjelovic, M., 2021. Recent genetic connectivity and clinal variation in chimpanzees. Communications Biology 4, 283.

Lobon, I., Tucci, S., de Manuel, M., Ghirotto, S., Benazzo, A., Prado-Martinez, J., Lorente-Galdos, B., Nam, K., Dabad, M., Hernandez-Rodriguez, J., Comas, D., Navarro, A., Schierup, M.H., Andres, A.M., Barbujani, G., Hvilsom, C., Marques-Bonet, T., 2016. Demographic history of the genus *Pan* inferred from whole mitochondrial genome reconstructions. Genome Biology and Evolution 8, 2020–2030.

Lovejoy, C.O., Latimer, B., Suwa, G., Asfaw, B., White, T.D., 2009. Combining prehension and propulsion: The foot of *Ardipithecus ramidus*. Science 326, 72–72e8.

Maisels, F., Strindberg, S., Greer, D., Jeffery, K., Morgan, D.L., Sanz, C., 2016. *Pan troglodytes* ssp. *troglodytes*. The IUCN Red List of Threatened Species, e.T15936A102332276.

Malenky, R.K., Wrangham, R.W., 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. American Journal of Primatology 32, 1–12.

Matsuzawa, T., Humle, T., Sugiyama, Y. (Eds.), 2011. The Chimpanzees of Bossou and Nimba, Primatology Monographs. Springer, Tokyo, Japan.

Matthews, J.K., Ridley, A., Niyigaba, P., Kaplin, B.A., Grueter, C.C., 2019. Chimpanzee feeding ecology and fallback food use in the montane forest of Nyungwe National Park, Rwanda. American Journal of Primatology 81, e22971.

McGrew, W.C., Baldwin, P.J., Tutin, C.E.G., 1988. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. American Journal of Primatology 16, 213–226.

McHenry, H.M., Jones, A.L., 2006. Hallucial convergence in early hominids. Journal of Human Evolution 50, 534–539.

Mitchell, M.W., Locatelli, S., Ghobrial, L., Pokempner, A., Clee, P.R.S., Abwe, E.E., Nicholas, A., Nkembi, L., Anthony, N.M., Morgan, B., Fotso, R., Peeters, M., Hahn, B., Gonder, M.K., 2015. The population genetics of wild chimpanzees in Cameroon and Nigeria suggests a positive role for selection in the evolution of chimpanzee subspecies. BMC Evolutionary Biology 15, 3.

Mitteroecker, P., Bookstein, F., 2011. Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. Evolutionary Biology 38, 100–114.
Mitteroecker, P., Gunz, P., 2013. Semilandmarks: A method for quantifying curves and surfaces. Hystrix 24, 103–109.
Morbeck, M.E., Zihlman, A.L., 1989. Body size and proportions in chimpanzees, with special reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania. Primates 30, 369–382.
Morgan, D., Sanz, C., Onononga, J.R., Strindberg, S., 2006. Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. International Journal of Primatology 27, 147–179.
Morin, P.A., Moore, J.J., Chakraborty, R., Jin, L., Goodall, J., Woodruff, D.S., 1994. Kin selection, social structure, gene flow, and the evolution of chimpanzees. Science 265, 1193–1201.
Musgrave, S., Lonsdorf, E., Morgan, D., Sanz, C., 2020. The ontogeny of termite gathering among chimpanzees in the Goualougo Triangle, Republic of Congo. American Journal of Physical Anthropology 174, 187–200.
Narat, V., Pennec, F., Simmen, B., Ngawolo, J.C.B., Krief, S., 2015. Bonobo habituation in a forest-savanna mosaic habitat: influence of ape species, habitat type, and sociocultural context. Primates; Journal of Primatology. 56, 339–349.
Nakamura, M., Nishida, T., 2012. Long-term field studies of chimpanzees at Mahale Mountains National Park, Tanzania. In: Kappeler, P.M., Watts, D.P. (Eds.), Long-Term Field Studies of Primates. Springer, Heidelberg, Germany. pp. 339–356.
Nishida, T., 1972. Preliminary information of the pygmy chimpanzees (*Pan paniscus*) of the Congo Basin. Primates 13, 415–425.
Nishida, T., Uehara, S., 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): Long term record from the Mahale Mountains, Tanzania. African Study Monographs 3, 109–130.
Norris, K., Asase, A., Collen, B., Gockowksi, J., Mason, J., Phalan, B., Wade, A., 2010. Biodiversity in a forest-agriculture mosaic – The changing face of West African rainforests. Biological Conservation 143, 2341–2350.
Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528.
Pennec, F., Krief, S., Hladik, A., Lubini Ayingweu, C., Bortolamiol, S., Bokika Ngawolo, J.-C., Narat, V., 2016. Floristic and structural vegetation typology of bonobo habitats in a forest-savanna mosaic (Bolobo Territory, D.R.Congo). Plant Ecology and Evolution 149, 199–215.
Piel, A.K., Strampelli, P., Greathead, E., Hernandez-Aguilar, R.A., Moore, J., Stewart, F.A., 2017. The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa valley, western Tanzania. Journal of Human Evolution 112, 57–69.
Pika, S., Klein, H., Bunel, S., Baas, P., Théleste, E., Deschner, T., 2019. Wild chimpanzees (*Pan troglodytes troglodytes*) exploit tortoises (*Kinixys erosa*) via percussive technology. Scientific Reports 9, 7661.
Pilbrow, V., 2006. Population systematics of chimpanzees using molar morphometrics. Journal of Human Evolution 51, 646–662.

Pontzer, H., Wrangham, R.W., 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: Implications for hominoid locomotor evolution. Journal of Human Evolution 46, 317–335 .

Prado-Martinez, J., Sudmant, P.H., Kidd, J.M., Li, H., Kelley, J.L., Lorente-Galdos, B., Veeramah, K.R., Woerner, A.E., O'Connor, T.D., Santpere, G., Cagan, A., Theunert, C., Casals, F., Laayouni, H., Munch, K., Hobolth, A., Halager, A.E., Malig, M., Hernandez-Rodriguez, J., Hernando-Herraez, I., Prüfer, K., Pybus, M., Johnstone, L., Lachmann, M., Alkan, C., Twigg, D., Petit, N., Baker, C., Hormozdiari, F., Fernandez-Callejo, M., Dabad, M., Wilson, M.L., Stevison, L., Camprubí, C., Carvalho, T., Ruiz-Herrera, A., Vives, L., Mele, M., Abello, T., Kondova, I., Bontrop, R.E., Pusey, A., Lankester, F., Kiyang, J.A., Bergl, R.A., Lonsdorf, E., Myers, S., Ventura, M., Gagneux, P., Comas, D., Siegismund, H., Blanc, J., Agueda-Calpena, L., Gut, M., Fulton, L., Tishkoff, S.A., Mullikin, J.C., Wilson, R.K., Gut, I.G., Gonder, M.K., Ryder, O.A., Hahn, B.H., Navarro, A., Akey, J.M., Bertranpetit, J., Reich, D., Mailund, T., Schierup, M.H., Hvilsom, C., Andrés, A.M., Wall, J.D., Bustamante, C.D., Hammer, M.F., Eichler, E.E., Marques-Bonet, T., 2013. Great ape genetic diversity and population history. Nature 499, 471–475.

Pruetz, J.D., 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, United Kingdom. pp. 161–182.

Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J.R., Walenz, B., Koren, S., Sutton, G., Kodira, C., Winer, R., Knight, J.R., Mullikin, J.C., Meader, S.J., Ponting, C.P., Lunter, G., Higashino, S., Hobolth, A., Dutheil, J., Karakoç, E., Alkan, C., Sajjadian, S., Catacchio, C.R., Ventura, M., Marques-Bonet, T., Eichler, E.E., André, C., Atencia, R., Mugisha, L., Junhold, J., Patterson, N., Siebauer, M., Good, J.M., Fischer, A., Ptak, S.E., Lachmann, M., Symer, D.E., Mailund, T., Schierup, M.H., Andrés, A.M., Kelso, J., Pääbo, S., 2012. The bonobo genome compared with the chimpanzee and human genomes. Nature 486, 527–531.

Pusey, A.E., Pintea, L., Wilson, M.L., Kamenya, S., Goodall, J., 2007. The contribution of long term research at Gombe National Park to chimpanzee conservation. Conservation Biology 21, 623–634.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org/.

Ramos, G.L., 2014. Positional behaviour of *Pan paniscus* at Lui Kotale, in the Democratic Republic of Congo. PhD dissertation, Indiana University, Bloomington, Indiana.

Reynolds, V., 2005. The Chimpanzees of the Budongo Forest: Ecology, Behaviour and Conservation. Oxford University Press, Oxford, United Kingdom.

Revell, L.J., 2009. Size-correction and principal components for interspecific comparative studies. Evolution; International Journal of Organic Evolution 63, 3258–3268.

Richmond, B.G., Begun, D.R., Strait, D.S., 2001. Origin of human bipedalism: The knuckle-walking hypothesis revisited. American Journal of Physical Anthropology 33, 70–105.

Robinson, C., Terhune, C.E., 2017. Error in geometric morphometric data collection: Combining data from multiple sources. American Journal of Physical Anthropology 164, 62–75.

Rohlf, F., Slice, D., 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic Zoology 39, 40–59.

Ruff, C.B., Burgess, M.L., Bromage, T.G., Mudakikwa, A., McFarlin, S.C., 2013. Ontogenetic changes in limb bone structural proportions in mountain gorillas (*Gorilla beringei beringei*). Journal of Human Evolution 65, 693–703.

Ruvolo, M., Disotell, T.R., Allard, M.W., Brown, W.M., Honeycutt, R.L., 1991. Resolution of the African hominoid trichotomy by use of a mitochondrial gene sequence. Proceedings of the National Academy of Sciences 88, 1570–1574.

Salem, A.-H., Ray, D.A., Xing, J., Callinan, P.A., Myers, J.S., Hedges, D.J., Garber, R.K., Witherspoon, D.J., Jorde, L.B., Batzer, M.A., 2003. Alu elements and hominid phylogenetics. Proceedings of the National Academy of Sciences 100, 12787–12791.

Schlager, S., 2017. Morpho and Rvcg – Shape Analysis in R. In: Zheng, G., Li, S., Szekely, G. (Eds.), Statistical Shape and Deformation Analysis. Academic Press, London. pp. 217–256.

Scholz, M.N., D'Août, K., Bobbert, M.F., Aerts, P., 2006. Vertical jumping performance of bonobo (*Pan paniscus*) suggests superior muscle properties. Proceedings of the Royal Society B: Biological Sciences. 273, 2177–2184.

Schultz, A.H., 1930. The skeleton of the trunk and limbs of higher primates. Human Biology 2, 303–438.

Schultz, A.H., 1934. Some distinguishing characters of the mountain gorilla. Journal of Mammalogy 15, 51–61.

Serckx, A., 2014. Eco-ethology of a population of bonobos (*Pan paniscus*) living in the western forest-savannah mosaics of the Democratic Republic of Congo. PhD dissertation, University of Liege, Liege, Belgium.

Serckx, A., Kühl, H.S., Beudels‐Jamar, R.C., Poncin, P., Bastin, J.-F., Huynen, M.-C., 2015. Feeding ecology of bonobos living in forest-savannah mosaics: Diet seasonal variation and importance of fallback foods. American Journal of Primatology 77, 948–962.

Shearer, B.M., Cooke, S.B., Halenar, L.B., Reber, S.L., Plummer, J.E., Delson, E., Tallman, M., 2017. Evaluating causes of error in landmark-based data collection using scanners. PLoS ONE 12, e0187452.

Slice, D.E. (Ed.), 2005. Modern Morphometrics in Physical Anthropology. Springer USA.

Stern, J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. American Journal of Physical Anthropology 60, 279–317.

Stratovan Corporation. Stratovan Checkpoint [Software]. Version 2018. 08.07. URL: https://www.stratovan.com/products/checkpoint.

Susman, R.L., 1984. The locomotor behavior of *Pan paniscus* in the Lomako Forest. In: Susman R.L. (Ed.), The Pygmy Chimpanzee: Evolutionary Biology and Behavior. Plenum Press, New York. pp. 369–393.

Susman, R.L., Badrian, N.L., Badrian, A.J., 1980. Locomotor behavior of *Pan paniscus* in Zaire. American Journal of Physical Anthropology 53, 69–80.

Takemoto, H., Kawamoto, Y., Furuichi, T., 2015. How did bonobos come to range south of the Congo river? Reconsideration of the divergence of *Pan paniscus* from other *Pan populations*. Evolutionary Anthropology 24, 170–184.

Terada, S., Nackoney, J., Sakamaki, T., Mulavwa, M.N., Yumoto, T., Furuichi, T., 2015. Habitat use of bonobos (*Pan paniscus*) at Wamba: Selection of vegetation types for ranging, feeding, and night-sleeping. American Journal of Primatology 77, 701–713.

Thorpe, S.K.S., Holder, R.L., Crompton, R.H., 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science 316, 1328–1331.

Tocheri, M.W., Solhan, C.R., Orr, C.M., Femiani, J., Frohlich, B., Groves, C.P., Harcourt-Smith, W.E., Richmond, B.G., Shoelson, B., Jungers, W.L., 2011. Ecological divergence and medial cuneiform morphology in gorillas. Journal of Human Evolution 60, 171–184.

Venkataraman, V.V., Kraft, T.S., Desilva, J.M., Dominy, N.J., 2013. Phenotypic plasticity of climbing-related traits in the ankle joint of great apes and rainforest hunter-gatherers. Human Biology 85, 309–328.

Waltenberger, L., Rebay-Salisbury, K., Mitteroecker, P., 2021. Three-dimensional surface scanning methods in osteology: A topographical and geometric morphometric comparison. American Journal of Physical Anthropology 174, 846–858.

Watts, D.P., 2012. Long-term field studies of chimpanzees at Mahale Mountains National Park, Tanzania. In: Kappeler, P.M., Watts, D.P. (Eds.), Long-Term Field Studies of Primates. Springer, Heidelberg, Germany. pp. 114–129.

Watts, D.P., Potts, K.B., Lwanga, J.S., Mitani, J.C., 2012. Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. American Journal of Primatology 74, 114–129.

Ward, C.V., 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: Where do we stand? American Journal of Physical Anthropology 35, 185–215.

Weber, G.W., Bookstein, F.L., 2011. Virtual Anthropology: A guide to a new interdisciplinary field. Springer-Verlag, Wien.

White, F.J., Wrangham, R.W., 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. Behaviour 105, 148–164.

Wilson, M.L., Lonsdorf, E.V., Mjungu, D.C., Kamenya, S., Kimaro, E.W., Collins, D.A., Gillespie, T.R., Travis, D.A., Lipende, I., Mwacha, D., Ndimuligo, S.A., Pintea, L., Raphael, J., Mtiti, E.R., Hahn, B.H., Pusey, A.E., Goodall, J., 2020. Research and conservation in the greater Gombe ecosystem, Uganda: Challenges and opportunities. Biological Conservation 252, 108853.

Zelditch, M., Swiderski, D., Sheets, H., Fink, W., 2004. Geometric Morphometrics for Biologists. Elsevier Academic Press, San Diego, California.

Zihlman, A.L., Stahl, D., Boesch, C., 2008. Morphological variation in adult chimpanzees (*Pan troglodytes verus*) of the Tai National Park, Cote D'Ivoire. American Journal of Physical Anthropology 135, 34–41.